RESOURCE PARTITIONING AMONG YOUNG-OF-YEAR SUNFISH (*Lepomis* spp.), AND PHENOTYPIC VARIATION OF BLUEGILLS (*L. macrochirus*)

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CHAPTER I

RESOURCE PARTITIONING AMONG YOUNG-OF-YEAR SUNFISH (Lepomis spp.)

Introduction

Although year class strength of many species of fish is determined during the egg and larval stages by physical factors such as wind and temperature operating over a relatively short period of time (Kramer and Smith 1962; Rupp 1965; Clady 1975; and others), it is unlikely that year class strength in sunfish (Lepomis spp.), which have prolonged spawning seasons, would be determined entirely by short term physical conditions. Species interactions may also play an important role in determining year class strength.

Because it is always profitable for species to avoid competition whenever possible (Pianka 1976), overt competition is rarely observed in established communities; instead, postcompetitive relationships, whereby coexisting species divide resources, are most evident. In a review, Schoener (1974) noted several major mechanisms of resource partitioning among coexisting species. Coexisting species usually segregate along one or more of the following niche dimensions: habitat, food, or time. Although most of the studies reviewed by Schoener (1974) were of terrestrial communities, numerous studies of resource partitioning among coexisting species in aquatic communities have been conducted since (Mendelson 1975; Ross 1977; Baker-Dittus 1978; Smart and Gee 1979;

and others). These studies have emphasized adult or subadult fish; more recently, George and Hadley (1979) studied resource partitioning between young-of-year (yoy) smallmouth bass (Micropterus dolomieui) and yoy rock bass (Ambloplites rupestris). Werner (1967) provided limited data that suggested yoy of four species of sunfish segregated, at least partially, along the habitat axis.

Nearly all studies of resource partitioning have examined how different species may avoid interspecific competition. Recently, several authors have examined resource allocation among age or size groups within a species (Keast 1977a; 1977b; 1978a; Matthews and Hill 1979; Jones 1981). Although fish growth in monotypic and polytypic populations is commonly density dependent (Buck and Thoits 1970; Cooper et al. 1971; Graham 1974), little attention has been given to intraspecific competition within a single cohort. Along with species interactions, intraspecific competition must play a dominant role in determining growth rates and year class strength in many species such as centrarchids, which have high fecundity and prolonged spawning seasons.

Because size (length or weight) is correlated with fecundity in most sunfish species (Morgan 1951; Larimore 1957; Wilbur 1969), growth rates can be used as a relative measure of fitness. Furthermore, in laboratory studies, size has been shown to be a significant factor in determining habitat and temperature selection, and who eats what, when, and where among bluegills (Casterlin and Reynolds 1978; Magnuson and Beitinger 1978). Therefore, size may also be correlated with fitness by directly affecting energy intake, metabolic rates, competitive ability, and survival.

Fish cohorts are subjected to a complex set of competitive

pressures. Interspecific (and perhaps intercohort) competition should generally tend to reduce a cohort's niche breadth (MacArthur and Wilson 1967); however, depending upon the pattern of exploitation, it can also increase niche breadth (Pianka 1976). Intense intracohort competition should tend to increase niche breadth. Roughgarden (1972) indicated that niche width has two components and a species (or cohort) can maintain a broad niche either by all individuals exploiting the same wide range of resource states (within phenotype component) or each individual can exploit few resource states, but different phenotypes in the population utilizing different resources (between phenotype component). In other words, the cohort can be made up of individuals acting as generalists in their utilization of resources, or each individual acting as a specialist but different phenotypes utilizing resources differently. Unfortunately, it is difficult to assess the relative magnitude of these two components in most previous studies of resource partitioning. However, Bryan and Larkin (1972) found evidence of phenotypic variation in food preferences of individually identifiable rainbow trout (Salmo gairdneri) that persisted for up to six months. Werner and Hall (1979) also found that among bluegills under competitive pressure there was a substantial amount of difference between individuals in the rate of habitat switching.

During the course of another study (Layzer and Clady in press), five species of yoy sunfish were collected from Lake Rush in southwestern Oklahoma. All five species were frequently collected together in a single seine haul. A cursory examination of the stomach contents from several individuals of each species indicated that similar food items were consumed by all species. Growth rates of centrarchids in Lake

Rush, particularly during their first year of life, are less than the average for Oklahoma (Mense 1976). I inferred that some resource (presumably food) was limiting fish production; however, if resources were limiting, partitioning should be evident to insure continued coexistence of these sunfishes.

I initiated the present study to resolve the apparent contradiction between my superficial observations of similar patterns of resource use by sympatric yoy sunfish, and competition theory which predicts partitioning of resources under a regime of a limited resource. Secondary objectives of my study were to: determine if habitat use by bluegills was correlated with fitness; determine if morphology of bluegills was similar in all habitats; and determine if natural selection affected morphological traits of bluegills.

CHAPTER II

STUDY AREA

This study was conducted in Lake Rush located in the Wichita Mountains National Wildlife Refuge in southwest Oklahoma. Recreational use of the refuge is high with most activity directed at wildlife observation and photography, hiking, and picnicking; however, moderately high fishing pressure is exerted on most refuge lakes.

Lake Rush is a 20.9 ha impoundment, formed by the construction of a dam on Blue Beaver Creek in 1936. Maximum depth of Lake Rush is about 10 m and the average depth is 4.8 m. Typically, flow from Blue Beaver Creek and other intermittent streams flowing into Lake Rush stops by early to mid July. The watershed of Blue Beaver Creek is a mixture of rolling prairie and rugged mountains composed of granite and gabbro. Wooded areas are dominated by post oak (Quercus stellata) and blackjack oak (Q. marilandica), with willows (Salix spp.) common along water edges. In a normal year evaporative loss from Lake Rush is 54 cm (measured as a decrease in lake level) but can reach 113 cm in a dry year (George Constantine, personal communication).

Lake Rush becomes thermally stratified by the middle of June, with near anoxic conditions in the hypolimnion (Table 1). Average Secchi disc reading was 1.45 $\pm$ .05 m during the summers of 1979 and 1980. Lake Rush has an elongated basin lying along an east-westerly line, with littoral areas primarily along the northern and southern shorelines. The

Table 1. Temperature and oxygen profiles for Lake Rush, summer, 1980.

Depth (m)	19 June		24 July		20 August	
	Temperature (°C)	DO (mg/liter)	Temperature (°C)	DO (mg/liter)	Temperature (°C)	DO (mg/liter)
0	28.9	7.2	27.8	6.1	23.3	6.9
1			27.2	5.8	22.2	6.5
2	28.3	7.5	27.2	5.0	22.2	6.2
3	20.6	3.4	26.7	5.0	22.2	6.0
4			22.7	1.0	20.0	2.5
5	16.7	2.1	16.7	0.5	15.0	1.5
6			14.4	0.3	12.2	1.0
7	13.9	1.9	13.3	0.2	11.1	0.8
8	12.7	1.7	12.7	0.1	10.0	0.5
9	12.2	1.7	12.7	0.1	10.0	0.5

southern shoreline of Lake Rush has a steeply sloping bottom, a firm, heterogeneous substrate composed of particles ranging from coarse sand to large boulders, and small isolated patches of water milfoil (Myriophyllum sp.). The northern side of the lake has a gently sloping, muck bottom, and dense aquatic macrophytes.

The distribution and composition of the submergent vegetation changed markedly between 1980 and 1981 as a result of an application of 2,4-D crystals by refuge personnel in April, 1981. In 1980, strikingly apparent zones of the plant community were each dominated by a single species. The emergent zone was 5 to 10 m wide and extended from the shoreline out to a depth of about 75 cm. This area was densely populated by spikerush (Eleocharis sp.). Unlike lakes with stable water levels, the emergent zone was bordered by a submergent zone 3 to 5 m wide, dominated by muskgrass (Chara sp.). This zone was apparently created by low lake levels which occur from late summer to early spring during most years. Contiguous with this zone and out to a depth of 1.8 to 2.5 m was a 30 to 60 m wide band of vegetation dominated by water milfoil. Pondweed (Potamogeton spp.), American lotus (Nelumbo lutea), and coontail (Ceratophyllum sp.), grew in small localized patches in this area. The final band of vegetation grew in a somewhat more irregular manner and was composed entirely of coontail, to a depth of 2.5 to 2.8 m. These water depths and associated plant distributions existed in 1980 only when the lake was full. Since the water source is primarily surface runoff, the lake level is dependent upon climatic factors. In 1979 and 1980, maximum lake level was in the spring and decreased throughout the summer, gradually exposing the emergent zone and most of the area dominated by Chara by early fall.

The herbicide, 2,4-D, was applied only over the submergent zone and virtually eliminated all of the water milfoil in 1981 but had little effect on coontail. In June, 1981, I noted dense patches of coontail in the same locations where it grew in 1980, including areas previously surrounded by water milfoil. The zone occupied by water milfoil in 1980 was gradually colonized by muskgrass in the shallower areas and by coontail in deeper areas during the summer of 1981 (see p 42).

During this and a concurrent study (Layzer and Clady in press), 19 species of fish were collected from Lake Rush (Table 2). Centrarchids made up 94 to 99% of spring and fall electrofishing samples, with bluegills and redear sunfish being the most abundant species collected.

Table 2. Species of fish collected from Lake Rush between 1979 and 1981.

Family	Species	Common name
Atherinidae	*Labidesthes sicculus*	Brook silversides
Centrarchidae	*Lepomis cyanellus*	Green sunfish
	L. gulosus	Warmouth
	L. macrochirus	Bluegill
	L. microlophus	Redear sunfish
	L. megalotis	Longear sunfish
	Micropterus salmoides	Largemouth bass
	Pomoxis nigromaculatus	Black crappie
Cyprinidae	*Hybognathus placitus*	Plains minnow
	Notemigonus crysoleucas	Golden shiner
	Notropis lutrensis	Redfin shiner
Ictaluridae	*Ictalurus melas*	Black bullhead
	I. natalis	Yellow bullhead
	I. punctatus	Channel catfish
Percidae	*Etheostoma spectabile*	Orangethroat darter
	Percina macrolepida	Bigscale logperch
Poeciliidae	*Gambusia affinis*	Mosquitofish

CHAPTER III

MATERIALS AND METHODS

Fish Collections

In 1980, sunfish were sampled during eight periods from June to October. In 1981, collections were made during seven periods from June to September. Each sampling period lasted for 2 to 5 days and periods were separated by 7 to 18 days. Fish were collected in bottom sets of unbaited cylindrical minnow traps (6.4 mm wire mesh) which had a funnel entrance (2.5 cm) at both ends. Initially traps were set for approximately 24 h, but beginning in mid-August, 1980, and continuing for the remainder of the study, traps were set for an average of 1.62 h (S.D. $\pm$ 0.53). When each trap was set, water depth was measured to the nearest 10 cm by using a metal measuring rod. Substrate and vegetation were determined visually in shallow areas. Substrates were classified as either fine (principally organic muck) or coarse (sand-rock). Vegetation was classified to genera using keys provided by Fassett (1969), and Muenscher (1967). In deep areas, substrate was determined by sounds transmitted by the metal measuring rod. Typically, substantial amounts of Myriophyllum or Ceratophyllum (the only plants occurring in deeper water) were retrieved with the traps.

Distances between adjacent traps varied considerably; however, minimal distances were approximately 15 m. Traps were set only in habitats which appeared to be homogeneous over an area of at least 10 m^2.

Fish collected from each trap were preserved separately in 10% formalin; later they were identified and total length measured to the nearest millimeter.

To identify the juveniles of species of Lepomis, I used descriptions and keys provided in Cross (1967), Miller and Robson (1973), Pfleiger (1975), as well as species-specific characteristics that I observed during the course of sorting and identifying several thousand yoy sunfish collected in another study (Layzer and Clady in press). I found that adult patterns of pigmentation were not always present in yoy sunfish. For example, only bluegills > 40 mm had a readily observable dark spot on the soft dorsal fin. The following is a summary of the most useful characteristics for identifying preserved specimens of species of yoy sunfish found in Lake Rush. Longear sunfish, green sunfish, and warmouth have short rounded pectoral fins compared to the long pointed pectoral fins of redear sunfish and bluegills. The large mouth of green sunfish and warmouth readily separated these two species from longears. Warmouth have several distinct dark lines radiating from the eye to the back of the head; most individuals also had broad vertical bars on the body. Green sunfish have neither lines on the head nor vertical bars on the body. Additionally, green sunfish have a prominent black spot near the posterior base of the dorsal fin. Redear sunfish and bluegills were separated on the basis of gill raker length and pigmentation. Bluegills have long, thin gill rakers, and 9 to 12 distinct vertical bars on their body. In contrast, redears have short gill rakers, and the vertical bars on the body deteriorate below the lateral line where the pattern is mottled. This is most evident for redears > 30 mm; redears > 45 mm do

not have any vertical bars.

Food Habits

Excepting six yoy green sunfish collected by electrofishing, all sunfish used in the food habits analysis were collected by minnow traps. Stomach contents of sunfish were examined under a dissecting microscope, and using keys from Pennak (1978) were identified to the lowest taxon consistently possible, and enumerated. Using an ocular micrometer, widths of all prey items in a stomach (up to a maximum of 20 of one type) were measured to the nearest 0.1 mm.

Plant Samples

In 1981, 20 plant samples were taken from the northern side of the lake during the middle of each month from June through August. Plants were collected to verify my field classification of vegetation types and to grossly estimate plant biomass. Samples were taken in each vegetational zone and at the following depth (cm) intervals: $\leq$ 50, 51-100, 101-150, 151-200. At each depth interval, 4 plant samples were obtained in the following manner. Using a measuring rod, the appropriate depth interval was first located from a canoe. I then tossed a 0.5 m diameter metal ring with a line and float attached. After positioning the canoe over the ring, I used the measuring rod to determine the depth and vegetation type. Plant samples were then obtained by diving and removing all of the plant material from inside the ring. Each sample was tagged and placed in a plastic bag, and refrigerated within 2 h. Within 36 h of collection, the plants were sorted to genus using keys from Muenscher (1967) and Fassett (1969),

blotted until all surface moisture was gone and then weighed. In shallower water, the above sampling procedure was modified only to the extent that the canoe was not used and vegetation types were visually classified.

Habitat Use

For analysis of depth utilization, I combined all the data for one year into six depth categories (resource states): <50, 100, 150, 200, 250, >250 cm. It was impossible to set an equal number of traps in each resource state, e.g. depth category, because the depth and vegetation dimensions were only partially independent of each other. For example, for some sampling periods three vegetation types were found within a single depth category, while other depths contained only two vegetation classes. To overcome this unequal sampling effort, I standardized the effort in the following manner. For each species, I calculated the catch per unit effort for each of the six depth categories:

$$CPUE_{ik} = \text{number of fish collected / number of traps set}$$

where $CPUE_{ik}$ is the mean number of species k collected in ith resource state. The proportion of use (p_{ik}) of a given resource state is then found by:

$$p_{ik} = CPUE_{ik} / \sum_{i}^{n} CPUE_{ik}$$

where n is the number of states in a resource set.

This same method of calculating the proportional use of a resource state was also used for the vegetation dimension. The p_{ik}'s obtained in this manner were then used for calculating niche breadth and overlap for each of the habitat dimensions. Niche breadth was calculated by the formula

of Levins (1968) as modified by Pianka (1973):

$$B = (1/\sum_{i}^{n} p_{ik}^2)/n$$

To determine the similarity in resource usage between pairs of species, I calculated a proportional overlap value (O; Schoener 1968):

$$O = 1 - 0.5 \sum_{i}^{n} | p_{ih} - p_{ik} |$$

This value measures the absolute area of the overlap of the two species resource utilization curves. Overlap values were computed only to facilitate discussion of the degree of similarity between species in their use of various resource sets.

Statistical Analysis

Trap catches were initially grouped by several variables such as year, depth categories, sampling period, etc. I calculated the index of dispersion (I) to determine if the sampling distribution for each species was random (Southwood 1978):

$$I = S^2(n - 1)/ \overline{X}$$

where $\overline{X}$ is the mean catch in the ith resource state ($CPUE_{ik}$); S^2 is the variance; and n is the number of traps set in the ith resource state. Comparison with the chi square distribution for n -1 df indicated that for most groupings, the trap catches were highly contagious. Taylor (1961) indicated that for organisms with a patchy distribution, the sampling variance and mean are related by the following power function:

$$S^2 = a\overline{X}^b$$

I grouped trap catches for yoy bluegills by sampling period and six depth categories, and calculated a separate mean and variance for each category. The means and variances were transformed to common logs (Taylor 1961), and a least squares regression line was fitted for each depth group. Analysis of covariance indicated no significant difference in slopes ($p > 0.05$). Therefore the data were combined to calculate a common slope of 1.346. Southwood (1978) suggested a square root transformation for sampling distributions where the exponent b of Taylor's power function (estimated by the above regression coefficient) equals 1 and a log transformation when $b = 2$. Attempts to stabilize the variance by the above transformations were unsuccessful (0.5 was added to each observation prior to using the square root transformation, and 1.0 was added for the log transformation). This procedure was also performed on catch data grouped only by year and depth category. Bartlett's test for homogeneity of variances (Steele and Torrie 1960) indicated significant differences among the variances in all cases ($p < 0.05$); consequently, catch data were analyzed by nonparametric methods following Conover (1971).

A chi square test for differences in probability distributions was used to test for differences in the depth and vegetational distributions among species. When more than 20% of the expected values in the contingency table were < 5, categories were combined in a meaningful way, e.g. adjacent depth categories. For each species, chi square goodness of fit tests were used to test the null hypothesis that the observed catch distribution was the same as the distribution of trapping effort i.e. densities are equal in all habitat categories. The calculated test statistic for all chi square tests is reported as a "T"

value to distinguish it from the true chi square distribution.

Bartlett's test was used to test for homogeneity of variances prior to all parametric tests. Comparisons of mean total length among species, and comparisons of total length within a species among different habitat classifications were made by the parametric t-test and analysis of variance (ANOVA). For ANOVA tests yielding significant differences ($p < .05$), Duncan's multiple range test was used to make further comparisons of mean total lengths.

CHAPTER IV

RESULTS

Relative Abundance

In 1980, a total of 1857 yoy sunfish were collected in minnow traps (Table 3). Bluegills and redear sunfish were codominant and together made up 91% of the total catch. These two species also dominated seine collections made in 1979 and 1980; however, bluegills were about twice as abundant as redear sunfish in the seine hauls. Differences in relative abundance between gears probably results from differences in size selectivity. For each of two sampling dates, I compared length frequency distributions for bluegills and redear sunfish collected by seine and minnow traps (Figures 1 and 2). Each of the four pairs of length distributions were significantly different ($p < 0.05$, Smirnov test), indicating differences in size selectivity between the two gears for bluegills and redear sunfish. Seines collected more small yoy bluegills (< 30 mm) while larger yoy bluegills were more abundant in trap catches (Figure 1). Minnow traps also tended to select for slightly larger redear sunfish (Figure 2); however, by late August, 1980, only 24% of the redear sunfish collected by seining were < 30 mm while 74% of the bluegills in seine hauls were < 30 mm. Moreover, the truncated distribution for bluegills collected by seining suggests that even by the middle of September they were not fully vulnerable to the mesh size. Bloom (1976) also found that minnow traps selected against

Table 3. Number and percent of total for each species of sunfish collected in traps and by seine from Lake Rush.

Specie	Seine				Minnow traps			
	1979		1980		1980		1981	
	Number	%	Number	%	Number	%	Number	%
Bluegills	2463	63.3	1355	61.7	853	45.9	1074	66.2
Redear sunfish	1270	32.6	817	37.2	839	45.2	381	23.5
Longear sunfish	104	2.7	8	0.4	75	4.0	62	3.8
Warmouth	45	1.2	11	0.5	82	4.4	100	6.2
Green sunfish	8	0.2	5	0.2	8	0.4	5	0.3

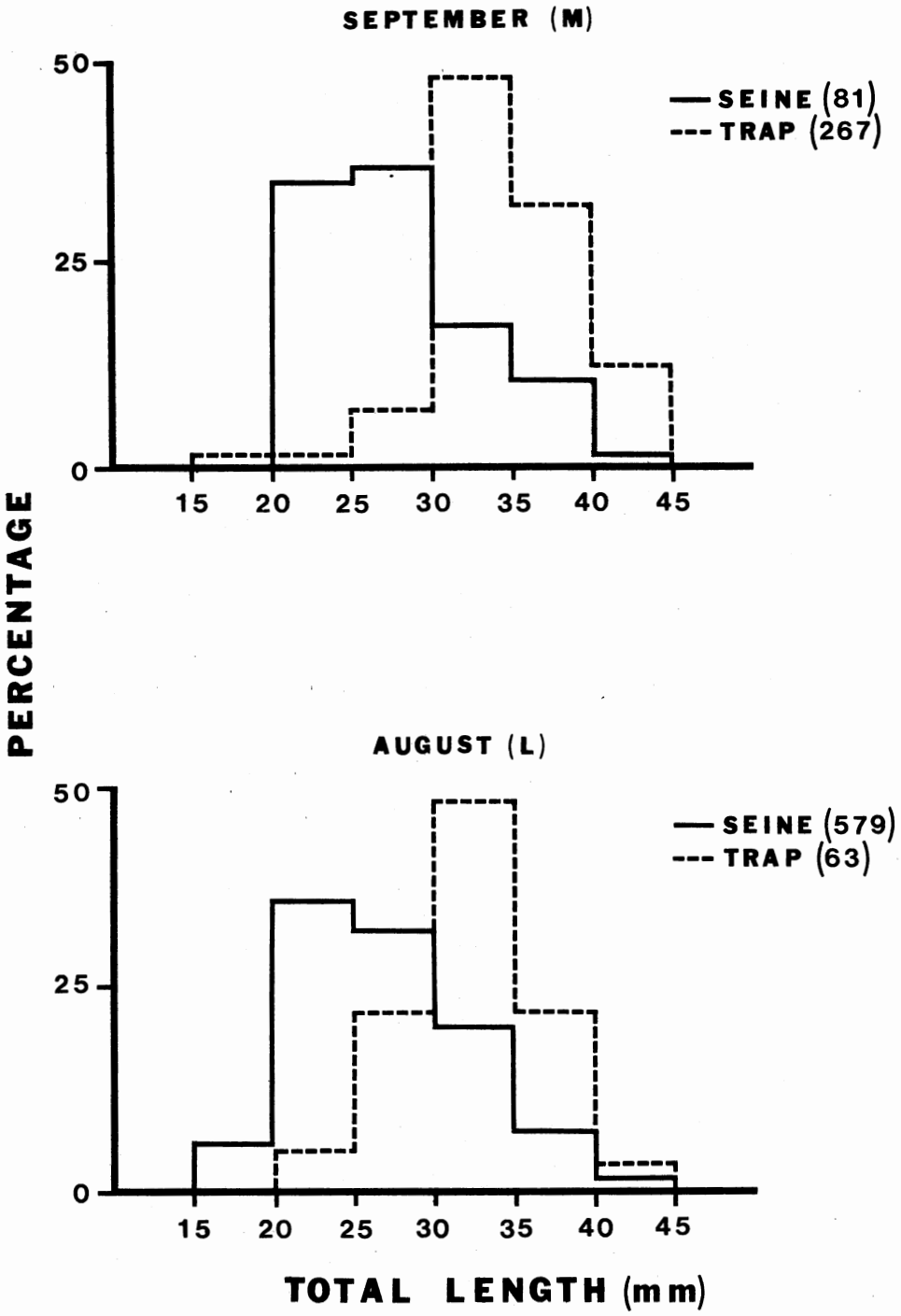

Figure 1. Length frequency distributions for two samples of yoy bluegills collected by seine and by minnow traps in 1980.

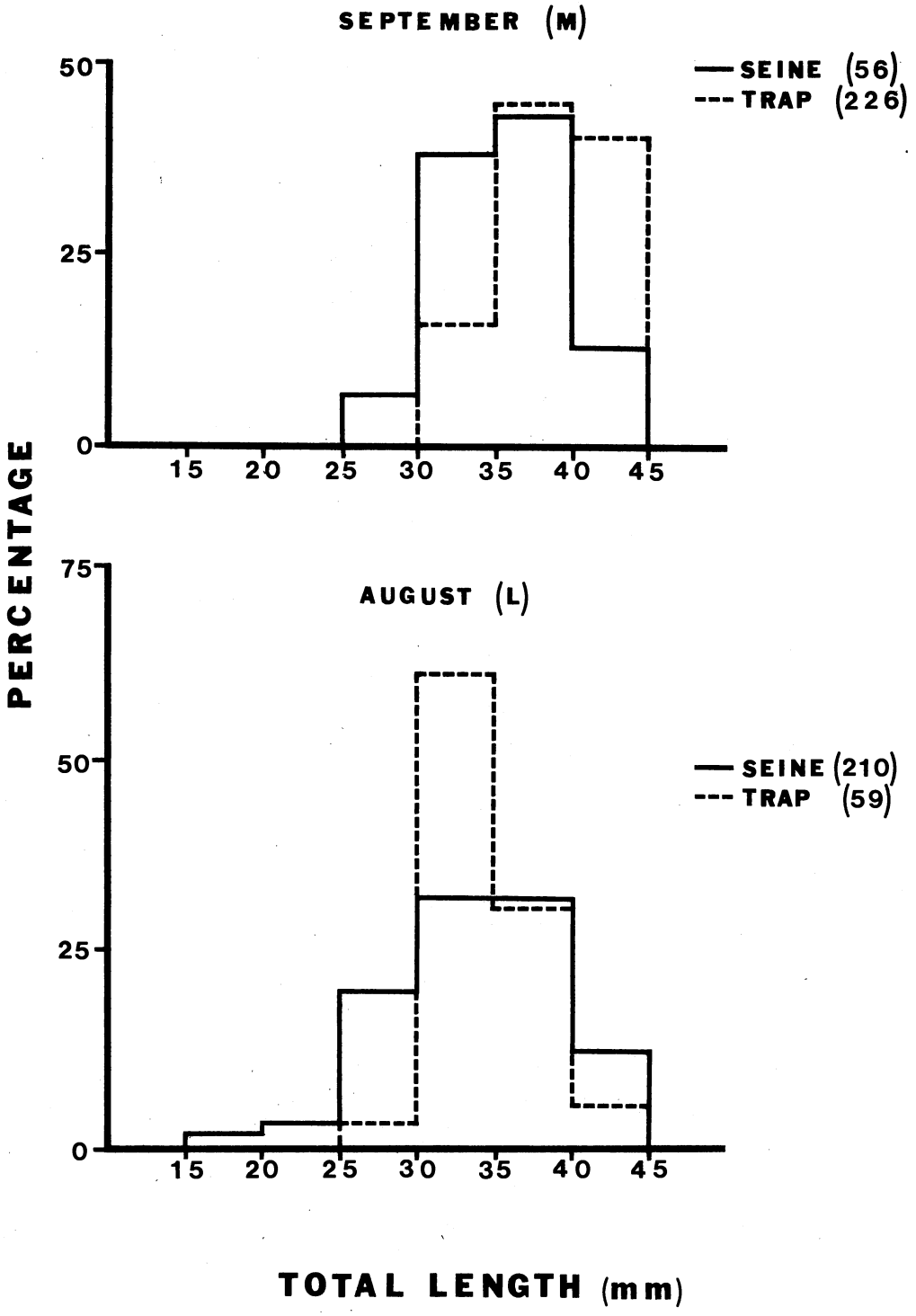

Figure 2. Length frequency distributions for two samples of yoy redear sunfish collected by seine and by minnow traps in 1980.

the small fish which were able to pass through the hardware cloth and selected against individuals too large to enter the trap opening. I did not find any evidence of selection against the largest yoy sunfish (<60 mm TL). In fact, minnow traps collected older fish of all species up to about 80 mm in length. Assuming that the only component of species selectivity for the two gears was size related, it appears that minnow traps underestimated the relative abundance of bluegills < 30 mm.

In 1981, a total of 1622 yoy sunfish was collected in minnow traps. Bluegills and redear sunfish again dominated, but bluegills were nearly three times more abundant than redear sunfish (Table 3). Changes in the relative abundance of species between years was primarily due to the significant decrease ($p < 0.001$) in density of redear sunfish in 1981 (Table 4). Density of longear sunfish also declined in 1981 ($p < 0.01$), but the densities of bluegills and warmouths remained constant between years ($p > 0.10$).

The numerical dominance of bluegills appears to be typical of many temperate lakes containing a mixed centrarchid fauna (Cooper et al. 1971; Keast and Harker 1977; Werner et al. 1977). Only rarely have other sunfish been reported to be more abundant than bluegills in the littoral fish community, e.g. Bull Shoals Reservoir (Applegate et al. 1967).

Seasonal Trends of Abundance

Young-of-year sunfish were first collected in minnow traps in late July, 1980 (Table 5). By early August, redear sunfish reached maximum densities and declined steadily throughout the summer. Because trap collections were biased towards larger individuals, I believe that

Table 4. Observed and, in parentheses, expected frequencies of yoy sunfish for each year, and catch per unit effort (CPUE). Expected frequencies were calculated assuming that the frequency of each species and trapping effort were the same.

Species	Year	Number of traps	Frequency	(CPUE)
Bluegill	1980	597	853 (830.04)	1.43
	1981	789	1074 (1096.96)	1.36
		T = 1.12 (1 df)	p > 0.10	
Redear sunfish	1980	597	839 (525.50)	1.41
	1981	789	381 (694.50)	0.48
		T = 328.55 (1 df)	p < 0.001	
Longear sunfish	1980	597	75 (59.01)	0.13
	1981	789	62 (77.99)	0.08
		T = 7.61 (1 df)	p < 0.01	
Warmouth	1980	597	82 (78.39)	0.14
	1981	789	100 (103.61)	0.13
		T = 0.13 (1 df)	p > 0.5	

Table 5. Mean number (± S.E.) of yoy sunfish collected per trap for each sampling period in 1980.

Sampling period*	Number of traps	Mean catch per trap				
		Bluegill	Redear sunfish	Longear sunfish	Warmouth	Green sunfish
June (M)	52					
July (L)	143	0.04 ± 0.02	1.89 ± 0.33	0.06 ± 0.02	0.08 ± 0.02	0.03 ± 0.01
August (E)	38	0.29 ± 0.17	2.16 ± 0.55	0.37 ± 0.13	0.71 ± 0.22	
August (M)	94	1.13 ± 0.23	1.22 ± 0.30	0.09 ± 0.05	0.20 ± 0.06	0.01 ± 0.01
August (L)	55	1.15 ± 0.23	1.07 ± 0.48	0.20 ± 0.09	0.02 ± 0.02	
September (M)	81	3.30 ± 0.59	3.06 ± 0.67	0.30 ± 0.11	0.17 ± 0.13	0.04 ± 0.03
October (E)	64	3.77 ± 0.78	0.66 ± 0.20	0.06 ± 0.03	0.09 ± 0.05	
October (L)	70	2.27 ± 0.40	0.33 ± 0.10	0.07 ± 0.04	0.06 ± 0.03	

* E = early; M = middle; L = late.

this decline reflects the cummulative effects of mortality. Although it is tempting to estimate mortality rates from these data, any such attempt would underestimate mortality because of the previously noted selection against smaller individuals, and more importantly, the continued recruitment to the sampling gear. In contrast to the trend of decreasing densities of redear sunfish, abundance of bluegills was low early in the season but steadily increased until early October.

Bluegills showed up earlier in the trap catches in 1981, but otherwise the pattern of increasing abundance was similar to 1980 (Table 6). In 1981, redear sunfish first appeared in trap catches in mid-July; densities then increased throughout the summer and reached a peak in early September. The different trends in abundance of redear sunfish between years suggest that fry hatched at a different time in 1981. Although adult redear sunfish were observed on nests in early April of both years, nests were deserted for an unknown period of time in 1981 when water temperatures dropped from 21 ^{o}C to 18 ^{o}C between April 9 and 10. During this same time, refuge personnel applied the herbicide 2,4-D to Lake Rush. Because this chemical affects reproduction in bluegills (Cope et al. 1970), it may have reduced reproductive success of redears early in 1981. On the other hand, male bluegills were also tending nests in April 1981 and all visible bluegill nests (in shallow water) were also deserted when the temperature dropped, yet they successfully reproduced during this same time period. (For a further discussion of bluegill spawning see p 126.)

Minnow traps were size selective, and their catches were influenced by two opposing factors: recruitment and mortality. Without making any assumptions regarding the mortality rate, it is likely that substantial

Table 6. Mean number (± S.E.) of yoy sunfish collected per trap for each sampling period in 1981.

Sampling period*	Number of traps	Mean catch per trap				
		Bluegill	Redear sunfish	Longear sunfish	Warmouth	Green sunfish
June (M)	123	0.04 ± 0.03				
July (E)	96	0.10 ± 0.04				
July (M)	142	0.43 ± 0.07	0.09 ± 0.03	0.02 ± 0.01	0.06 ± 0.02	
August (E)	142	1.54 ± 0.17	0.44 ± 0.09	0.15 ± 0.04	0.15 ± 0.04	0.02 ± 0.01
August (M)	96	1.97 ± 0.29	0.86 ± 0.18	0.22 ± 0.08	0.21 ± 0.05	
September (E)	94	2.81 ± 0.35	1.28 ± 0.22	0.10 ± 0.05	0.15 ± 0.05	0.02 ± 0.02
September (L)	96	3.41 ± 0.45	1.07 ± 0.23	0.08 ± 0.04	0.36 ± 0.11	

* E = early; M = middle; L = late.

mortality occurred throughout both seasons, resulting in decreasing fish densities over time. However, recruitment to the gear would be related to several factors, most important of which would be the duration and intensity of the spawning season. If fish spawned over a prolonged time period and the recruitment rate exceeded the mortality rate, then yoy densities should have continued to increase over time. Because successful reproduction of redear sunfish occurred later in 1981, redear yoy were not subjected to mortality for as long a time period as they were in 1980. Thus, even though bluegills continued to increase in the trap catches throughout the season each year and redear sunfish increased throughout 1981, individuals in these populations may have died at rates similar to those which apparently caused the decline in redear sunfish densities in 1980. No discernible pattern of abundance was apparent for longear sunfish, warmouth, and green sunfish during either year. These species were uncommon, and any fluctuations were relatively small and may have resulted from the combined effects of recruitment, mortality, and sampling error.

Size of Sunfish

Mean lengths of bluegills collected at depths ranging from 51 to 150 cm were frequently less than the average size of bluegills collected in shallower or deeper areas (Table 7). This phenomenon was most pronounced in 1981, when analysis of variance indicated significant differences ($p < 0.002$) in length among fish from different depths during 4 of 5 sampling periods. Similarly, redear sunfish were smaller at intermediate depths in 1981, but not in 1980 (Table 8). Since differences in mean length were small, and all depths were sampled each

Table 7. Results of analysis of variance and Duncan's multiple range test for differences in mean total length of bluegills collected in three depth categories during each sampling period. Mean lengths underscored by a common line are not significantly different ($p > 0.05$). [S = shallow ($\leq$ 50 cm); I = intermediate (51-150 cm); D = deep (> 150 cm); E = early; M = middle; L = late].

Sampling period	Depth and length			ANOVA statistics		
				F	df	p
1980						
August (M)	(S) 32.6	(D) 31.5	(I) 29.9	5.41	2,104	<0.006
August (L)	(I) 32.3	(S) 31.2	(D) 29.3	2.29	2,60	>0.10
September (M)	(S) 34.2	(D) 33.0	(I) 33.0	2.19	2,264	>0.10
October (E)	(S) 36.4	(D) 36.3	(I) 34.1	1.98	2,239	>0.10
October (L)	(D) 34.0	(I) 34.0	(S) 33.7	0.12	2,156	>0.80
1981						
July (M)	(I) 30.0	(S) 29.7	(D) 28.5	2.48	2,58	>0.05
August (E)	(S) 31.9	(D) 31.0	(I) 30.0	6.68	2,215	<0.002
August (M)	(S) 32.9	(I) 30.9	(D) 30.6	6.63	2,186	<0.002
September (E)	(S) 33.6	(D) 33.0	(I) 31.7	7.92	2,262	<0.001
September (L)	(D) 35.0	(S) 33.6	(I) 33.1	6.43	2,324	<0.002

Table 8. Results of analysis of variance and Duncan's multiple range test for differences in mean total length of redear sunfish collected in three depth categories during each sampling period. Mean lengths underscored by a common line are not significantly different ($p > 0.05$). [S = shallow ($\leq$ 50 cm); I = intermediate (51-150 cm); D = deep (> 150 cm); E = early; M = middle; L = late].

Sampling period	Depth and length			ANOVA statistics		
				F	df	p
1980						
July (L)	(S) 31.3	(I) 30.9		1.43	1,268	>0.20
August (E)	(D) 34.0	(I) 33.7	(S) 33.4	0.06	2,79	>0.90
August (M)	(I) 34.5	(S) 33.5	(D) 29.0	1.97	2,112	>0.10
August (L)	(I) 35.8	(S) 33.2		3.40	1,57	=0.07
September (M)	(S) 39.7	(D) 38.3	(I) 37.2	0.92	2,245	>0.40
1981						
August (E)	(S) 37.6	(D) 36.9	(I) 36.0	1.11	2,59	>0.30
August (M)	(D) 39.6	(S) 38.9	(I) 35.5	6.66	2,80	<0.01
September (E)	(D) 40.2	(S) 39.3	(I) 36.5	5.11	2,117	<0.01
September (L)	(S) 44.2	(D) 43.4	(I) 40.0	4.96	2,100	<0.01

period, mean total lengths for all data combined were probably the best estimate of mean size of fish for each period.

Except for the two earliest samples in 1980, total lengths of yoy sunfish were significantly different ($p < 0.002$) among all species during each period (Table 9 and 10). Almost invariably, the average size of bluegills was less than the mean lengths of the other species. Ranking by size of the other species changed between samples and frequently their mean lengths were not significantly different ($p > 0.05$).

Changes in mean length between samples cannot be attributed to growth alone for much the same reasons that changes in density cannot be used to estimate mortality rates. Continued recruitment of smaller individuals and mortality of larger individuals would lower the average size of fish collected. I have estimated average growth rates for bluegills from the rings on their otoliths (see Table 61). In general, these growth rates exceed those that would be estimated based on changes in mean length between samples.

Time of Activity

Minnow traps are a passive gear which rely on fish movement, so catch rates can be used as a measure of fish activity. I combined trap catches into five 3 h time periods according to the times traps were set. Incidental observations made during the course of my study suggested that many of the fish collected in a trap entered it shortly after the trap was set. For example, on one occasion I set a trap in shallow water and almost immediately observed fish entering it; the trap was retrieved after 7 minutes and it contained 21 fish. In addition,

Table 9. Results of analysis of variance and Duncan's multiple range test for differences in mean total length among species for each sampling period in 1980. Mean lengths underscored by the same line are not significantly different ($p > 0.05$). BG = bluegills; RE = redear sunfish; LE = longear sunfish; WM = warmouth; GS = green sunfish; E = early; M = middle; L = late.

Sampling period	Species and length					ANOVA statistics		
						F	df	p
July (L)	RE 31.3	WM 30.9	LE 30.2	BG 29.9		2.02	3, 291	>0.10
August (E)	RE 33.4	WM 32.7	LE 32.6	BG 31.3		2.14	3, 130	>0.05
August (M)	GS 43.0	RE 33.7	LE 32.9	WM 31.5	BG 31.4	7.93	4, 245	<0.0001
August (L)	LE 36.0	RE 33.5	BG 31.6	WM 28.0		7.13	3, 130	<0.002
September (M)	LE 39.8	GS 39.7	RE 39.7	WM 37.5	BG 33.9	54.44	4, 551	<0.0001
October (E)	RE 43.6	LE 43.0	WM 37.2	BG 36.3		32.69	3, 289	<0.0001
October (L)	LE 43.4	WM 40.8	RE 39.1	BG 33.8		16.02	3, 187	<.0001

Table 10. Results of analysis of variance and Duncan's multiple range test for differences in mean total length among species for each sampling period in 1981. Mean lengths underscored by the same line are not significantly different ($p > 0.05$). BG = bluegills; RE = redear sunfish; LE = longear sunfish; WM = warmouth; GS = green sunfish; E = early; M = middle; L = late.

Sampling period	Species and length				ANOVA statistics		
					F	df	p
July (M)	WM 33.2	LE 32.3	RE 31.6	BG 29.6	7.35	3, 82	<0.0002
August (E)	RE 36.9	LE 34.3	WM 33.6	BG 30.9	44.74	3, 320	<0.0001
August (M)	RE 37.8	WM 35.8	LE 34.3	BG 31.5	51.02	3, 309	<0.0001
September (E)	LE 40.0	WM 38.5	RE 37.7	BG 32.3	54.14	3, 403	<0.0001
September (L)	RE 42.1	LE 41.5	WM 40.7	BG 33.7	86.40	3,469	<0.0001

escapement over time has been documented for other types of passive sampling gear (Hansen 1944; Patriarche 1968). Since no information is available concerning escapment from minnow traps, I arbitrarily included in the analysis only those traps set for < 3 h.

For all sunfish, greatest periods of activity occurred either in the morning or late in the day, while lowest catch rates for all species were during the middle of the afternoon (Table 11). Werner (1969) found that peak catches of bluegill larvae were made approximately 1 h after dusk with a lesser peak near sunrise, and a minimum at midday. Reynolds and Casterlin (1976) maintained larger bluegills under an LD 12:12 photoperiod and found that at 31 ^{o}C bluegill activity was greatest near the onset of the light period and gradually decreased until dark.

Activity of warmouth was greatest in late afternoon, evening, and early morning. This suggests that warmouth may be either crepuscular or perhaps even more nocturnal in their habits. Since traps were rarely set and lifted after dark, I have no direct information on nocturnal activity of these fishes.

Depth Utilization

Use of depth was significantly different ($p < 0.001$) among species each year (Tables 12 and 13). For each year, results of chi square goodness of fit tests indicated that the observed distributions of each species was significantly different than the distribution of sampling effort (Tables 14, 15, 16, and 17). Thus the observed depth distributions for each species were not functions of unequal trapping effort. Each species also had distinct patterns of depth utilization which differed between years (Figure 3). In 1980, all species except

Table 11. Proportion (adjusted for trapping effort) of each species collected during each 3 h time interval.

Time interval[a]	Species				
	Bluegill	Redear sunfish	Longear sunfish	Warmouth	Green sunfish
≤ 0900	0.15	0.14	0.28	0.16	
0901 - 1200	0.18	0.27	0.26	0.13	0.35
1201 - 1500	0.15	0.12	0.05	0.14	
1501 - 1800	0.33	0.26	0.27	0.30	
> 1800	0.19	0.21	0.15	0.27	0.65

[a]Traps fished for less than 3 h.

Table 12. Observed and, in parentheses, expected frequencies of yoy sunfish in each depth category. Expected frequencies were calculated assuming equal probabilities of depth utilization among species in 1980.

	Depth interval (cm)			
Species	≤ 50	51 - 100	101 - 150	> 150
Bluegill	585 (648.17)	123 (100.57)	51 (45.21)	94 (59.05)
Redear sunfish	746 (637.53)	60 (98.92)	22 (44.47)	11 (58.08)
Longear sunfish	52 (56.99)	19 (8.84)	3 (3.98)	1 (5.19)
Warmouth	22 (62.31)	16 (9.67)	22 (4.35)	22 (5.68)

$T = 280.47$ (9 df) $p < 0.001$

Table 13. Observed and, in parentheses, expected frequencies of yoy sunfish in each depth category. Expected frequencies were calculated assuming equal probabilities of depth utilization among species in 1981.

	Depth interval (cm)				
Species	$\leq$ 50	51 - 100	101 - 150	151 - 200	> 200
Bluegill	262 (294.90)	244 (255.71)	290 (261.03)	213 (201.91)	65 (60.44)
Redear sunfish	153 (104.62)	121 (90.71)	61 (92.60)	39 (71.63)	7 (21.44)
Longear sunfish	24 (17.02)	6 (14.76)	22 (15.07)	10 (11.66)	0 (3.49)
Warmouth	5 (27.46)	14 (23.81)	20 (24.30)	42 (18.80)	19 (5.63)

$T = 174.79$ (12 df) $p < 0.001$

Table 14. Observed and, in parentheses, expected frequencies of yoy bluegills in each depth category. Expected frequencies were calculated assuming that the distributions of bluegills and trapping effort were the same.

Year	Depth (cm)	Number of traps	Frequency	CPUE
1980	$\leq$ 50	250	585 (357.20)	2.34
	51 - 100	168	123 (240.04)	0.73
	101 - 150	90	51 (128.59)	0.57
	151 - 200	43	68 (61.44)	1.58
	201 - 250	18	16 (25.72)	0.89
	> 250	28	10 (40.01)	0.36
		T = 219.48 (5 df)	$p < 0.001$	
1981	$\leq$ 50	229	262 (311.72)	1.14
	51 - 100	201	244 (273.60)	1.21
	101 - 150	140	290 (190.57)	2.07
	151 - 200	158	213 (215.07)	1.35
	> 200	61	65 (83.03)	1.07
		T = 66.95 (4 df)	$p < 0.001$	

Table 15. Observed and, in parentheses, expected frequencies of yoy redear sunfish in each depth category. Expected frequencies were calculated assuming that the distributions of redear sunfish and trapping effort were the same.

Year	Depth (cm)	Number of traps	Frequency	CPUE
1980	$\leq$ 50	250	746 (351.34)	2.98
	51 - 100	168	60 (236.10)	0.36
	101 - 150	90	22 (126.48)	0.24
	151 - 200	43	6 (60.43)	0.14
	201 - 250	18	5 (25.30)	0.28
	> 250	28	0 (39.35)	0.00
		T = 765.65 (5 df)	$p < 0.001$	
1981	$\leq$ 50	229	153 (110.58)	0.66
	51 - 100	201	121 (97.06)	0.60
	101 - 150	140	61 (67.60)	0.44
	151 - 200	158	39 (76.30)	0.25
	> 200	61	7 (29.46)	0.11
		T = 58.16 (4 df)	$p < 0.001$	

Table 16. Observed and, in parentheses, expected frequencies of yoy longear sunfish in each depth category. Expected frequencies were calculated assuming that the distributions of longear sunfish and trapping effort were the same.

Year	Depth (cm)	Number of traps	Frequency	CPUE
1980	$\leq$ 50	250	52 (31.41)	0.21
	51 - 100	168	19 (21.11)	0.11
	101 - 150	90	3 (11.31)	0.03
	151 - 200	43	1 (5.40)	0.02
	201 - 250	18	0 (2.26)	0.00
	> 250	28	0 (3.52)	0.00
		T = 29.19 (5 df)	$p < 0.001$	
1981	$\leq$ 50	229	24 (17.99)	0.10
	51 - 100	201	6 (15.79)	0.03
	101 - 150	140	22 (11.00)	0.16
	151 - 200	158	10 (12.42)	0.06
	> 200	61	0 (4.79)	0.00
		T = 24.34 (4 df)	$p < 0.001$	

Table 17. Observed and, in parentheses, expected frequencies of yoy warmouth in each depth category. Expected frequencies were calculated assuming that the distributions of warmouth and trapping effort were the same.

Year	Depth (cm)	Number of traps	Frequency	CPUE
1980	$\leq$ 50	250	22 (34.34)	0.09
	51 - 100	168	16 (23.08)	0.10
	101 - 150	90	22 (12.36)	0.24
	151 - 200	43	19 (5.91)	0.44
	201 - 250	18	2 (2.47)	0.11
	> 250	28	1 (3.85)	0.04
		T = 43.83 (5 df)	$p < 0.001$	
1981	$\leq$ 50	229	5 (29.02)	0.02
	51 - 100	201	14 (25.48)	0.07
	101 - 150	140	20 (17.74)	0.14
	151 - 200	158	42 (20.03)	0.27
	> 200	61	19 (7.73)	0.32
		T = 65.87 (4 df)	$p < 0.001$	

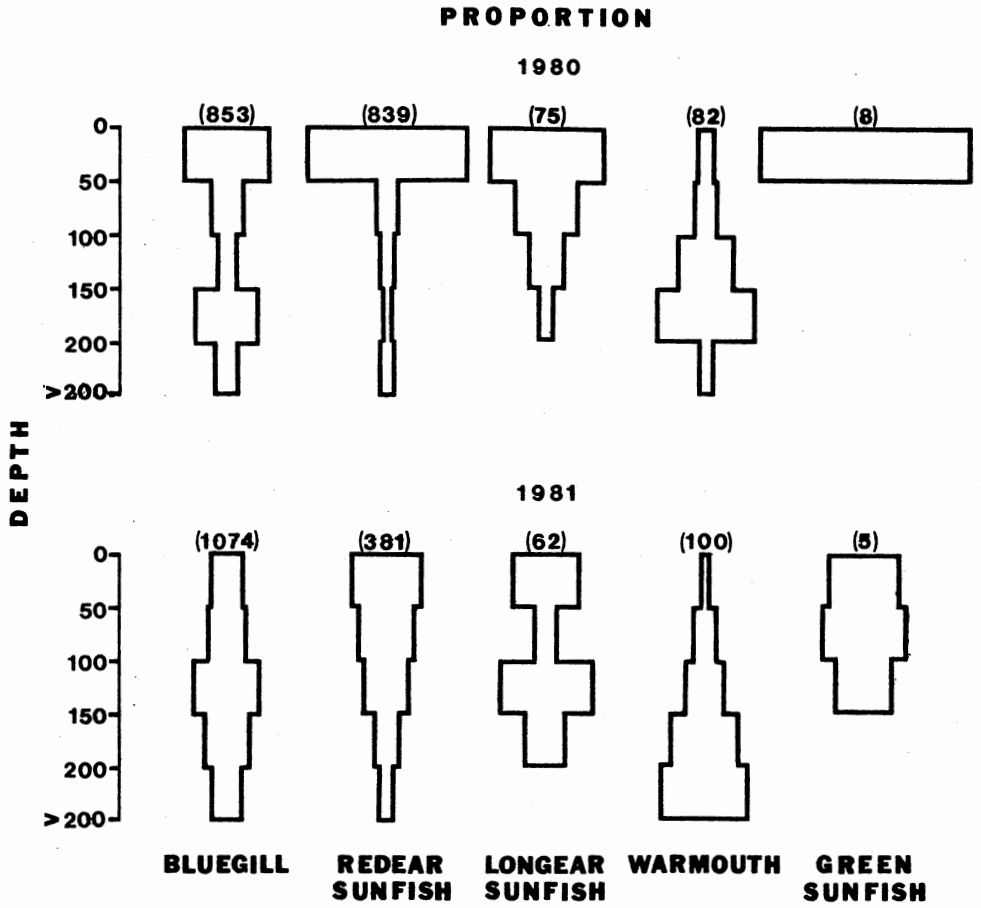

Figure 3. Depth distributions of five species of sunfish collected in minnow traps. Sample sizes are in parentheses.

warmouth were caught more frequently in traps set at depths of 50 cm or less. Bluegills had a distinctly bimodal distribution, with high abundances at the shallowest depth and between 151 and 200 cm. For the most part, the distribution of warmouth, with maximum abundance at greater depths, was complementary to the distributions of the other species. In 1981, all species moved towards deeper water. For example, the proportion of redear sunfish at depths 50 cm or less was only .32 in 1981 compared to .75 in 1980; however, the distribution of redear sunfish was inversely related to depth each year. Longear sunfish preferred decidedly different depths each year; in 1980 their distribution was unimodal and inversely related to depth, while in 1981 they had a bimodal distribution and were most abundant at depths between 101 and 150 cm. The distribution of warmouth, though more similar between years than that of other species, also shifted towards deeper water in 1980.

Most other studies of depth distribution of centrarchids deal only with larval stages (Werner 1967; 1969) or with I+ and older fish. However, in most instances the depth distributions of older fish is similar to that observed for yoy in my study. Werner et al. (1977) found the greatest abundance of older warmouths at depths of 1.5 to 1.7 m, while green sunfish were distributed along the shore at depths < 1.0 m, and longear sunfish were more common at depths < 1.0 m. However, Laughlin and Werner (1980) reported that small longear sunfish (similar in size to yoy in Lake Rush) were more abundant at depths between 1 and 4 m. Young-of-year bluegills appear to have the least restrictive depth requirements. Casterlin and Reynolds (1978) found in laboratory studies that yoy bluegills equally preferred areas which simulated deep,

nonvegetated water, and shallow, vegetated water.

Plant Samples

In addition to classifying each zone by the dominant species, I further divided (subjectively) areas of Ceratophyllum into dense and sparse stands. Early in the season, differences in Ceratophyllum biomass were striking, dense stands frequently reached the surface, while sparse stands were usually not visible from the surface. All vegetation samples were dominated by a single species (except those intentionally taken in areas classified as having no vegetation; Table 18), in fact, most samples contained only one species. Although samples taken in Eleocharis stands often contained small amounts (< 20 g/m^2) of other species, these species usually were not attached to the substrate and apparently had drifted inshore from other areas. Eleocharis and dense stands of Ceratophyllum had the greatest biomass, and their biomass changed little over the summer. In contrast, Chara grew rapidly between June and July, and also colonized vast areas that were dominated by Myriophyllum in 1980. Similarly, the sparse stands of Ceratophyllum first appeared in July, primarily in areas where Myriophyllum grew in 1980. Further colonization by Ceratophyllum and Chara occurred until August when nearly all of the suitable (fine substrate) habitat was occupied. Additionally, in many areas, sparse stands of Ceratophyllum grew rapidly between July and August, and entered the "dense" Ceratophyllum category.

Utilization of Vegetation

Because the dominant vegetation types grew in definite zones

Table 18. Species composition and biomass of aquatic macrophytes in samples collected in 1981. (D = dense; S = sparse).

Month	N	Habitat Classification	Mean biomass (kg/m^2)					
			Ceratophyllum	Eleocharis	Chara	Isoetes	Myriophyllum	Elodea
June	4	Chara			0.34			
	4	Ceratophyllum (D)	6.13					
	4	Eleocharis	<0.01	6.87			<0.01	<0.01
	4	Isoetes				0.13		
	4	No vegetation	0.02					
July	8	Chara	0.01		2.33			
	2	Ceratophyllum (D)	8.70					
	2	Ceratophyllum (S)	2.46					
	4	Eleocharis		5.98			0.02	
	4	No vegetation						
August	8	Chara			2.54			
	4	Ceratophyllum (D)	8.29					
	4	Ceratophyllum (S)	1.22				<0.01	
	2	Eleocharis		5.14	<0.01		<0.01	
	2	No vegetation	0.01					

directly related to depth, distribution of fish in the vegetation, with few exceptions, was largely a function of depth utilization. For instance, in 1980 redear sunfish were caught more frequently in traps set in Eleocharis sp. and Chara sp. (Table 19). These plants were the dominant vegetation over most of the season at depths less than 51 cm, which was the depth category most utilized by redear sunfish.

Although some plants occurred at more than one depth during each month, and all plants did over the entire season, there was little evidence of specific associations between fish and vegetation. On the contrary, the data suggest that in most instances, fish responded to depth independently of vegetation. For example in mid-August, 1980, 52% of the bluegills were collected in Chara sp. and only 15% in Myriophyllum sp. During this period, Chara was restricted to depths less than 101 cm. For the same period, 49% of the bluegills were caught at depths less than 101 cm. By mid-September 1980, decreasing lake levels totally eliminated the Chara; at that time, Myriophyllum was the only abundant plant in water less than 101 cm deep. Correspondingly, 54% of the bluegills were collected at depths less than 101 cm, and 53% of the bluegills were found in Myriophyllum. The only evidence of selection for specific vegetation was the preference ($p < 0.001$) of warmouth for dense (biomass > 8 kg/m^2) versus sparse (biomass < 3 kg/m^2) stands of Ceratophyllum (Table 20). Other virtual cases of selection for specific vegetation, independent of depth, appear to be artifacts of the method used to calculate the proportion of use. The apparent selection of Najas by most species in 1981 is an obvious example. Najas was not collected between June and August. I first observed low densities of Najas early in September in the Chara zone. By late

Table 19. Proportional use (adjusted for trapping effort) of vegetation types by yoy sunfish in Lake Rush in 1980 and 1981.

Vegetation	Species				
	Bluegill	Redear sunfish	Longear sunfish	Warmouth	Green sunfish
1980					
Ceratophyllum spp.	0.28	0.03		0.22	
Chara spp.	0.14	0.49		0.08	0.28
Eleocharis spp.	0.05	0.26	0.07	0.06	0.64
Isoetes spp.	0.14				
Myriophyllum spp.	0.31	0.10	0.04	0.05	0.08
Nelumbo lutea		0.10		0.58	
None	0.08	0.02	0.89	0.01	
1981					
Ceratophyllum spp. (dense)	0.19	0.07	0.09	0.54	
Ceratophyllum spp. (sparse)	0.20	0.05	0.21	0.18	
Chara spp.	0.11	0.17	0.06	0.11	0.42
Eleocharis spp.	0.07	0.04	0.05	0.02	0.48
Najas spp.	0.40	0.65	0.40	0.12	
None	0.03	0.02	0.19	0.03	0.10

Table 20. Observed and, in parentheses, expected frequencies of yoy sunfish in dense and sparse patches of Ceratophyllum. Expected frequencies were calculated assuming equal utilization of both vegetation types in 1981.

Species	Dense		Sparse		T	df	p
Bluegill	301	(303.90)	187	(184.10)	0.073	1	>0.50
Redear sunfish	52	(47.33)	24	(28.67)	1.222	1	>0.25
Longear sunfish	6	(8.72)	8	(5.28)	2.249	1	>0.10
Warmouth	59	(44.22)	12	(26.78)	13.100	1	<0.001

September, in one area sampled, the Chara had disappeared and Najas was dominant. Because traps were set in Najas during only one sampling period, at the end of the season when fish densities were greatest (Table 6), this single estimate of use of Najas is biased upwards.

To avoid such apparent biases in the data, I collapsed all vegetation classes into two categories: vegetated and nonvegetated areas. There are several major advantages to this simplified classification scheme. Firstly, it eliminates the dependency of vegetation on depth, and hence the redundancy of information. Thereby the two habitat dimensions become orthogonal since, within the depth range sampled, the presence or absence of vegetation is independent of depth. Secondly, in describing niche relationships among species, it is highly desirable to weight each resource state by its availability (Hurlburt 1978; Petraitis 1979; Lawlor 1980). Because I did not measure relative availability of each vegetation type, and because it was obvious that large differences occurred in relative abundance of each plant species, the collapsed categories more closely approximated each other in area since the presence of vegetation was largely confined to one side of the lake. Thirdly, by collapsing the vegetation classification, sample size per category is increased and should reduce other sampling biases. Chi square tests for differences in probability of use of vegetated and nonvegetated areas indicated highly significant differences ($p < 0.001$) among species each year (Tables 21 and 22). Only longear sunfish occurred more frequently than expected in nonvegetated areas (Tables 23 and 24). Of course the danger in collapsing vegetation classes is that the resulting resolution is too coarse to detect the possible existence of a much finer partitioning of

Table 21. Observed and, in parentheses, expected frequencies of yoy sunfish in vegetated and nonvegetated habitats. Expected frequencies were calculated assuming equal probabilities of use among species in 1980.

Year	Species	Vegetation	
		Present	Absent
1980	Bluegill	732 (742.28)	121 (110.72)
	Redear sunfish	793 (730.10)	46 (108.90)
	Longear sunfish	5 (65.27)	70 (9.73)
	Warmouth	79 (71.36)	3 (10.63)
		T = 477.88 (3 df) p <0.001	

Table 22. Observed and, in parentheses, expected frequencies of yoy sunfish in vegetated and nonvegetated habitats. Expected frequencies were calculated assuming equal probabilities of use among species in 1981.

		Vegetation	
Year	Species	Present	Absent
1981	Bluegill	943 (925.88)	131 (148.12)
	Redear sunfish	333 (328.46)	48 (52.54)
	Longear sunfish	26 (53.45)	36 (8.55)
	Warmouth	92 (86.21)	8 (13.79)
		T = 107.79 (3 df) p <0.001	

Table 23. Observed and, in parentheses, expected frequencies of yoy sunfish in vegetated and nonvegetated habitats. Expected frequencies were calculated assuming that the distributions of each species and trapping effort were the same in 1980.

Species	Habitat	Number of traps	Frequency	CPUE
Bluegill	Vegetated	397	732 (567.24)	1.84
	Nonvegetated	200	121 (285.76)	0.61
	T = 142.86 (1 df) p <0.001			
Redear sunfish	Vegetated	397	793 (557.93)	2.00
	Nonvegetated	200	46 (281.07)	0.23
	T = 295.64 (1 df) p <0.001			
Longear sunfish	Vegetated	397	5 (49.87)	0.01
	Nonvegetated	200	70 (25.13)	0.35
	T = 120.49 (1 df) p <0.001			
Warmouth	Vegetated	397	79 (54.53)	0.20
	Nonvegetated	200	3 (27.47)	0.02
	T = 32.78 (1 df) p <0.001			

Table 24. Observed and, in parentheses, expected frequencies of yoy sunfish in vegetated and nonvegetated habitats. Expected frequencies were calculated assuming that the distributions of each species and trapping effort were the same in 1981.

Species	Habitat	Number of traps	Frequency	CPUE
Bluegill	Vegetated	481	943 (654.74)	1.96
	Nonvegetated	308	131 (419.26)	0.43
	T = 325.10 (1 df) p <0.001			
Redear sunfish	Vegetated	481	333 (232.27)	0.69
	Nonvegetated	308	48 (148.73)	0.12
	T = 111.90 (1 df) p <0.001			
Longear sunfish	Vegetated	481	26 (37.80)	0.05
	Nonvegetated	308	36 (24.20)	0.12
	T = 9.43 (1 df) p <0.001			
Warmouth	Vegetated	481	92 (60.96)	0.19
	Nonvegetated	308	8 (39.04)	0.03
	T = 40.49 (1 df) p <0.001			

habitat. However, as will become apparent, a finer resolution of vegetation is unneccessary to adequately explain the coexistence of sunfish in Lake Rush.

Prey Utilization

Although seasonal trends in prey abundance and fish diets have frequently been documented (Seaburg and Moyle 1964; Wilbur 1969; Mittlebach 1981a; and others), I did not observe any trends in the diets within or between species over time. However, the relative and absolute importance of various prey items did fluctuate between sampling periods for a given species and between species for the same sampling period. Similarly, Keast (1977a) found diets of small bluegills to be quite constant over the summer.

The mean number of prey per fish showed similar fluctuations (Table 25). However, the average number of prey per stomach was significantly greater (t-tests, all p's $\leq$ 0.0008) in 1981 compared to 1980 for each species (Table 26). Examination of the diets of individual fish collected during a single sampling period revealed that similar differences in prey numbers and types occurred among individuals also. This suggests that dietary differences between sampling periods may have resulted from chance. Inclusion in a sample of one or more individuals that fed extensively on a prey type that was of minor importance in the diets of other fish in the sample could greatly influence the overall apparent diet of a species.

To further explore this possibility, I examined in detail the diets of bluegills collected in mid-August, 1981 (Table 27). I selected this sample for the following reasons: it contained the most bluegills for

Table 25. Mean number (± S.E.) of prey items in stomachs of sunfish containing food, presented for each sampling period. E = early; M = middle; L = late.

Sampling period	Species				
	Bluegills	Redear sunfish	Longear sunfish	Warmouth	Green sunfish
1980					
July (L)	8.6 ± 4.0	3.0 ± 1.0	9.5 ± 6.2	2.3 ± 0.9	1.5 ± 0.5
August (E)	16.3 ± 6.1	16.7 ± 5.3	3.1 ± 0.9	16.5 ± 8.9	11.5 ± 9.5
August (M)	19.5 ± 6.2	15.7 ± 7.6	20.0 ± 6.7	5.9 ± 1.6	4.0
August (L)	44.6 ± 12.0	27.0 ± 16.1	7.8 ± 1.7		
September (M)	5.6 ± 0.8	24.6 ± 10.2	13.7 ± 3.1	12.2 ± 5.1	1.0
October (E)	10.0 ± 6.6	19.9 ± 6.7	24.3 ± 2.3	3.3 ± 1.7	
October (L)	13.1 ± 3.1	28.9 ± 9.6	29.6 ± 11.7	1.0	

Table 25 (continued).

Sampling period	Species				
	Bluegills	Redear sunfish	Longear sunfish	Warmouth	Green sunfish
1981					
June (M)	8.0				
July (E)	31.8 ± 7.5				
July (M)	25.5 ± 6.8	19.8 ± 5.4	31.0	17.0 ± 6.2	
August (E)	35.6 ± 8.7	39.3 ± 14.3	59.9 ± 14.3	19.6 ± 13.3	10.5 ± 2.5
August (M)	81.4 ± 25.8	27.8 ± 11.3	64.8 ± 8.0	42.8 ± 27.1	20.3 ± 2.4
September (E)	139.1 ± 29.6	55.5 ± 15.2	177.3 ± 48.8	3.5 ± 1.4	166.5 ± 163.5
September (L)	60.0 ± 10.3	66.0 ± 21.1	77.9 ± 18.0	35.6 ± 5.0	

Table 26. Average number of prey items in stomachs of sunfish. Statistical tests were performed on log transformed data.

Species	Geometric mean number of prey/fish 1980	1981	t	df	p
Bluegill	6.23	32.19	-7.5561	150	0.0001
Redear sunfish	1.29	19.50	-5.1528	149	0.0001
Longear sunfish	5.15	62.31	-11.2309*	103	0.0001
Warmouth	5.91	21.27	-4.3064*	83.2	0.0001
Green sunfish	1.69	7.11	-4.1266	16	0.0008

*Unequal variances, approximate t-test used.

Table 27. Frequency of food items in stomachs of individual bluegills collected in mid-August, 1981.

	Prey category					
Fish number	*Daphnia*	Chydoridae	Ostracoda	Copepoda	Chironomidae	Other
1	2	3	4	14	1	1
2	0	9	11	1	0	0
3	0	0	0	0	0	0
4	1	16	10	26	2	5
5	0	8	10	6	9	2
6	0	0	7	1	2	4
7	0	1	0	0	0	0
8	0	3	43	33	5	2
9	0	0	163	5	2	6
10	1	239	21	2	55	1
11	170	11	2	5	7	2
12	0	11	18	4	8	0
13	0	25	9	0	8	1
14	2	18	7	5	2	6

any sample collected in 1981; frequency of occurrence (number of fish containing a particular item) was high for most prey categories, thus reducing the variance among individuals in the types of prey consumed; and the mean number of prey per fish was high. From this sample of 14 fish, I took five random samples of eight fish each and calculated a percent similarity index (Schoener's overlap x 100%; Whittaker and Fairbanks 1958) for each of the 10 possible pairs of samples. Excluding the sample from June, 1981, which contained only eight prey items, I also compared the similarity in bluegill diets between the 36 possible pairs of sampling periods within years. Similarity of bluegill diets between sampling periods averaged 64% and ranged from 31 to 94%, while the average similarity of the five random samples from August, 1981, averaged 71% and ranged from 45 to 97%. This difference in average similarity of the two data sets is remarkably small, particularly when my criteria for selecting the August sample should have resulted in greater similarity among the random samples, especially since many of the same individuals appeared in all five random samples. Because the variation within samples appears to be similar to the variation among samples, the observed changes in diets between sampling periods may simply reflect variation in diets among individuals.

To determine if diet changed with size, I separated each species into two size groups (< 30 and ≥ 30 mm TL) and compared their diets (Tables 28 and 29). The diets of the two groups were quite similar. The only notable difference was that more fish less than 30 mm long consumed Daphnia, but in the case of bluegills this difference was not consistent between years. Therefore, the combined data are probably representative of the diet of yoy sunfish > 20 mm long (the smallest

Table 28. Frequency of occurrence (%) of major prey items in small (< 30 mm) and large (≥ 30 mm) yoy sunfish in 1980.

Species	Size (mm)	N	Prey				
			Daphnia	Chydorids	Ostracods	Copepods	Chironomids
Bluegill	< 30	19	37	58	63	42	74
	≥ 30	71	23	28	46	27	68
Redear sunfish	< 30	9	11	11	56	11	67
	≥ 30	88	9	32	68	31	51
Longear sunfish	< 30	8	25	25	63	13	38
	≥ 30	54	0	48	65	9	46
Warmouth	< 30	10	30	10	20	20	50
	≥ 30	59	17	5	24	15	31

Table 29. Frequency of occurrence (%) of major prey items in small (< 30 mm) and large (≥ 30 mm) yoy sunfish in 1981.

Species	Size (mm)	N	Prey				
			Daphnia	Chydorids	Ostracods	Copepods	Chironomids
Bluegill	< 30	17	23	71	71	71	88
	≥ 30	45	47	73	76	73	89
Redear sunfish	< 30	0					
	≥ 30	54	20	31	93	39	50
Longear sunfish	< 30	4	50	75	75	75	100
	≥ 30	39	31	87	100	87	100
Warmouth	< 30	4	50	10	50	100	75
	≥ 30	44	32	25	34	57	61

size examined).

Since diets varied little with size of fish, and also varied within a sample as much as between samples, I combined all food habits data by year. Yearly diets of sunfish encompassed a broad array of prey items, ranging from zooplankton to sedentary pelecypods (Tables 30 and 31). All species of sunfish consumed similar prey items though frequently in greatly different proportions. A total of 24 types of food were identified from stomach contents; however, five prey types generally accounted for over 90% of the food items (Figure 4). In both years, ostracods were the most abundant food in both redear sunfish and longear sunfish. Ostracods were the primary food of warmouths only in 1980. In 1981, warmouths consumed relatively more cladocerans and copepods.

Diets of fish are often a reflection of the habitat where fish live. For example, Keast and Welch (1968) noted that bluegill diets were related to both time of day and water depth at capture. From knowledge of specific prey-habitat associations, Werner and Hall (1979) were able to determine habitat utilization of individual sunfish from their stomach contents. For each sampling period I randomly selected individuals for stomach analysis with the view of obtaining a broad and representative sample over time and habitat. Therefore, my study was not designed to provide abundant data on dietary differences over time or between habitats. Of course, it would be more productive to simultaneously examine diets over time and within a framework of a multi-dimensional habitat classification. Sample sizes in the present study preclude such a fine analysis of diet. An alternative approach, and one that I believe still provides considerable insight, is to successively examine the relationship between diet and one variable at a

Table 30. Numbers of food items found in yoy sunfish stomachs in 1980.

Taxon	Species				
	Bluegill	Redear sunfish	Longear sunfish	Warmouth	Green sunfish
Arachnoidea					
Hydracarina	17	7	1	1	1
Crustacea					
Copepoda	91	66	16	40	3
Chydoridae	383	335	137	5	1
Daphnia sp.	157	11	3	44	17
Decapoda	2				
Ostracoda	271	979	437	133	2
Hyalella azteca	2	1	2	2	
Gastropoda	5				
Diptera					
Chironomidae	251	206	83	124	3
Chaoboridae		1		1	
Cerratopogonidae	6	7			
Tabanidae					
Coleoptera					
Haliplus sp.	1				
Ephemeroptera					
Caenis sp.	8	2		6	
Stenonema sp.			1		
Odonata					
Anisoptera	5	4	1	2	3
Zygoptera	8	1			
Hemiptera	8	1		1	
Trichoptera	4			1	
Megaloptera					
Sialis sp.					
Unidentified insects	6	3			

Table 30 (continued).

Taxon	Species				
	Bluegill	Redear sunfish	Longear sunfish	Warmouth	Green sunfish
Oligochaeta	3				1
Pelecypoda					
Sphaeriidae				1	
Osteichthyes					
Lepomis sp.			1		
Rotatoria					
Number of stomachs examined	90	97	62	69	10
Number of empty stomachs	10	21	13	31	4

Table 31. Numbers of food items found in yoy sunfish stomachs in 1981.

Taxon	Species				
	Bluegill	Redear sunfish	Longear sunfish	Warmouth	Green sunfish
Arachnoidea					
Hydracarina	52	5	32		1
Crustacea					
Copepoda	623	71	310	245	21
Chydoridae	954	39	583	18	123
Daphnia sp.	599	24	41	521	
Decapoda	3			3	
Ostracoda	568	1883	2111	49	250
Hyalella azteca	7		2	5	2
Gastropoda	7	9	9	11	1
Diptera					
Chironomidae	848	172	664	116	24
Chaoboridae			2	47	
Cerratopogonidae	18	7	19		
Tabanidae					
Coleoptera					
Haliplus sp.	1				
Ephemeroptera					
Caenis sp.	29	5	5	15	4
Stenonema sp.			1		
Odonata					
Anisoptera	3	4		1	4
Zygoptera	7		1	2	1
Hemiptera	8	1		1	
Trichoptera	4	8	8	3	
Megaloptera					
Sialis sp.	1				
Unidentified insects	18	8	8	2	

Table 31 (continued).

Taxon	Species				
	Bluegill	Redear sunfish	Longear sunfish	Warmouth	Green sunfish
Oligochaeta	3	1	9		1
Pelecypoda					
Sphaeriidae		1	2		
Osteichthyes					
Lepomis sp.			1	2	
Rotatoria	2		12		3
Number of stomachs examined	62	54	43	48	8
Number of empty stomachs	3	1	0	8	0

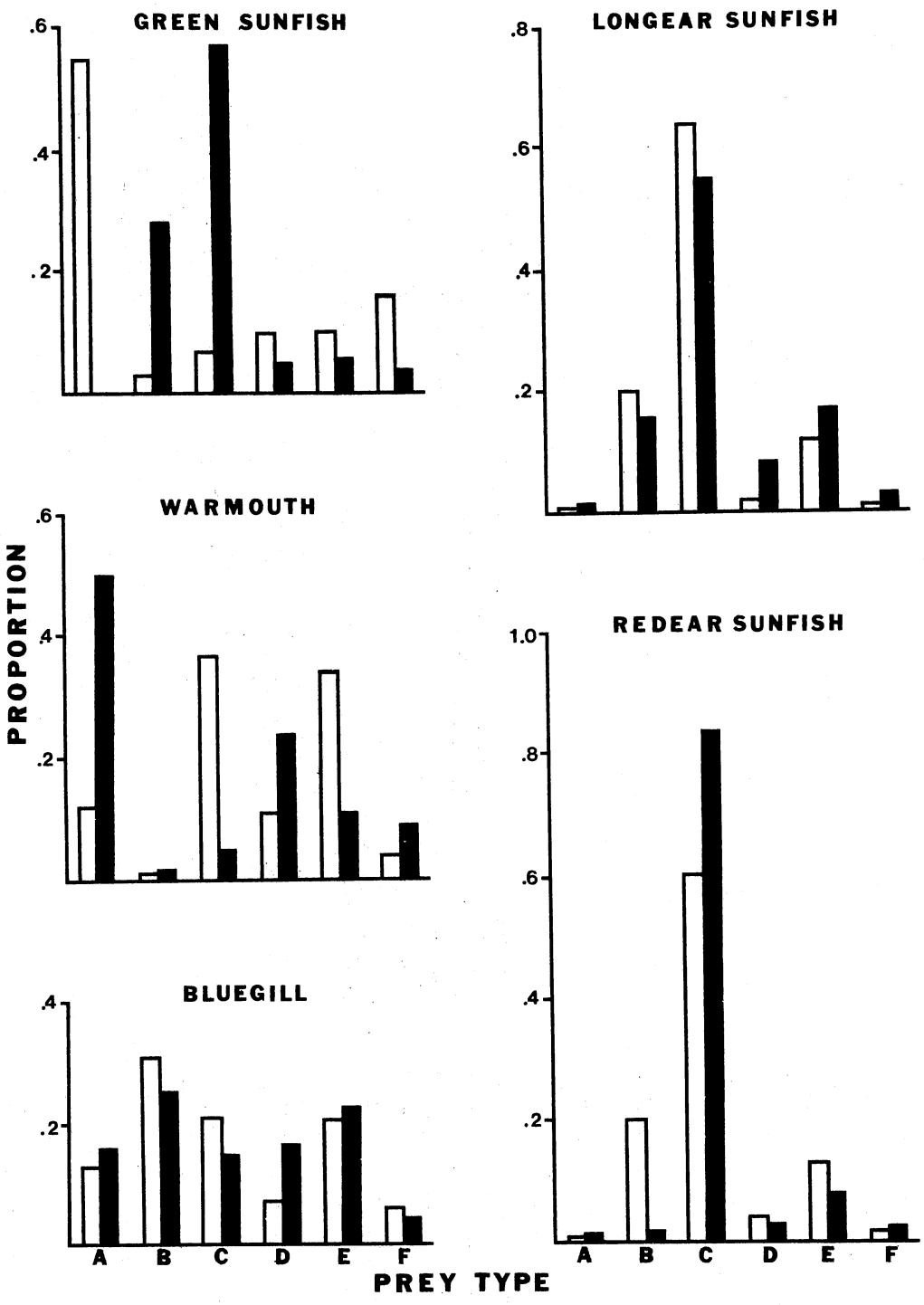

Figure 4. Proportion of diets of sunfish that were made up of various invertebrates. (open bars, 1980; solid bars, 1981; A = Daphnia; B = Chydoridae; C = Ostracoda; D = Copepoda; E = Chironomidae; F = other).

time. It should be kept in mind that in some cases small sample size may be the underlying cause of apparent differences, and also this method of analysis masks interactions between variables. Nevertheless, parallel trends observed between years or across species are probably indicative of real differences in diet. For these analyses, I used broad habitat and time classifications to increase sample size.

For all species, diets were surprisingly similar over time of day (Tables 32 and 33). Although diets of most species varied slightly with time of day, these variations were not consistent trends that occurred in both years. Greatest divergence in diets was associated with small sample sizes.

Depths at capture were grouped into three broad categories: shallow ($\leq$50 cm), intermediate (51 -149 cm), and deep ($\geq$ 150 cm). While redear sunfish and longear sunfish showed either no consistent trend or differed little in their use of ostracods at different depths, ostracods were clearly more important in the diet of bluegills from deep water (Tables 34 and 35). In contrast, ostracods were more important in the diet of warmouth inhabiting shallow water compared to the diets of fish collected at greater depths. In general, chydorids made up a greater proportion of the diets of most species collected in shallower areas. Use of other prey types did not show any consistency over depth between years; however, the small number of fish collected in deep water and used for analysis in 1980, may have obscured other dietary differences. Moreover, changes in the plant community between years may have had a very pronounced effect on prey distribution or vulnerability, particularly in intermediate and deep water areas, where the changes in macrophytes occurred.

Table 32. Proportionate abundance of prey items in diets of sunfish collected at different times in 1980. Morning = ≤ 1100 hours; Afternoon = 1101 - 1800 hours; Evening = > 1800 hours.

Species	N	Mean number of prey/fish (± S.E.)	Time group	Proportion of diet					
				Daphnia	Ostracoda	Chironomidae	Copepoda	Chydoridae	Other
Bluegill	10	19.4 ± 6.9	Morning	0.07	0.25	0.33	0.21	0.12	0.02
	69	11.9 ± 2.7	Afternoon	0.15	0.18	0.18	0.04	0.40	0.05
	11	19.5 ± 6.2	Evening	0.08	0.35	0.19	0.09	0.17	0.12
Redear sunfish	28	10.0 ± 6.1	Morning	<0.01	0.87	0.07	0.03	0.02	
	57	20.4 ± 3.9	Afternoon	<0.01	0.52	0.13	0.05	0.28	0.02
	12	15.3 ± 7.7	Evening	0.02	0.73	0.17	0.02	0.04	0.02
Longear sunfish	19	6.5 ± 1.7	Morning	0.02	0.63	0.10		0.23	0.01
	36	11.6 ± 2.5	Afternoon		0.78	0.07	0.01	0.13	0.01
	7	20.0 ± 6.7	Evening		0.23	0.28	0.07	0.40	0.02
Warmouth	18	1.3 ± 1.0	Morning		0.13	0.29	0.46		0.13
	38	7.5 ± 2.8	Afternoon	0.07	0.46	0.32	0.09	0.01	0.04
	13	4.1 ± 1.4	Evening	0.43		0.47	0.06	0.02	0.02

Table 33. Proportionate abundance of prey items in diets of sunfish collected at different times in 1981. Morning = ≤ 1100 hours; Afternoon = 1101 - 1800 hours; Evening = > 1800 hours.

Species	N	Mean number of prey/fish (± S.E.)	Time group	Proportion of diet					
				Daphnia	Ostracoda	Chironomidae	Copepoda	Chydoridae	Other
Bluegill	27	50.6 ± 9.5	Morning	0.28	0.24	0.17	0.13	0.14	0.05
	17	41.4 ± 9.9	Afternoon	0.06	0.11	0.27	0.20	0.34	0.02
	18	93.1 ± 23.6	Evening	0.10	0.10	0.26	0.18	0.32	0.05
Redear sunfish	14	20.9 ± 20.9	Morning	0.01	0.88	0.03	0.02	0.04	0.02
	21	56.0 ± 14.8	Afternoon	0.01	0.88	0.04	0.03	0.02	0.02
	19	40.5 ± 7.5	Evening	0.01	0.76	0.16	0.04	<0.01	0.03
Longear sunfish	17	125.4 ± 29.4	Morning	<0.01	0.71	0.12	0.07	0.08	0.01
	17	64.8 ± 9.7	Afternoon	0.02	0.36	0.22	0.09	0.25	0.05
	9	65.2 ± 14.1	Evening	0.01	0.35	0.27	0.10	0.22	0.05
Warmouth	13	33.4 ± 8.5	Morning	0.56	0.04	0.09	0.13	0.02	0.17
	9	24.2 ± 7.4	Afternoon	0.09	0.09	0.21	0.53	0.03	0.05
	26	14.9 ± 9.8	Evening	0.66	0.03	0.08	0.19	0.01	0.03

Table 34. Proportionate abundance of prey items in diets of sunfish collected at different depths in 1980. Shallow = ≤ 50 cm; Intermediate = 51 - 150 cm; Deep = > 150 cm.

Species	N	Mean number of prey/fish (± S.E.)	Depth category	Proportion of diet					
				Daphnia	Ostracoda	Chironomidae	Copepoda	Chydoridae	Other
Bluegill	56	11.2 ± 2.4	Shallow	0.03	0.19	0.24	0.06	0.41	0.08
	30	14.6 ± 4.6	Intermediate	0.29	0.18	0.16	0.05	0.26	0.05
	4	41.0 ± 18.8	Deep	0.07	0.46	0.19	0.20	0.07	0.01
Redear sunfish	78	16.6 ± 3.5	Shallow	0.01	0.55	0.14	0.04	0.25	0.02
	18	18.4 ± 6.3	Intermediate	0.01	0.80	0.09	0.03	0.05	0.02
	1	1.0	Deep		1.00				
Longear sunfish	44	11.4 ± 2.3	Shallow	<0.01	0.58	0.14	0.03	0.24	0.01
	18	10.1 ± 2.3	Intermediate	0.01	0.81	0.07	0.01	0.10	<0.01
	0		Deep						
Warmouth	23	7.3 ± 4.1	Shallow	0.05	0.62	0.16	0.11	0.02	0.04
	25	2.9 ± 0.9	Intermediate	0.33	0.16	0.27	0.18	0.01	0.04
	21	5.8 ± 2.7	Deep	0.09	0.15	0.64	0.07	0.00	0.05
Green sunfish	10	3.1 ± 2.0	Shallow	0.55	0.06	0.10	0.10	0.03	0.16
	0		Intermediate						
	0		Deep						

Table 35. Proportionate abundance of prey items in diets of sunfish collected at different depths in 1981. Shallow = ≤ 50 cm; Intermediate = 51 - 150 cm; Deep = > 150 cm.

Species	N	Mean number of prey/fish (± S.E.)	Depth category	Proportion of diet					
				Daphnia	Ostracoda	Chironomidae	Copepoda	Chydoridae	Other
Bluegill	19	41.1 ± 9.4	Shallow	0.16	0.15	0.16	0.15	0.33	0.04
	30	74.9 ± 15.7	Intermediate	0.16	0.10	0.25	0.18	0.27	0.04
	13	55.2 ± 13.8	Deep	0.17	0.30	0.22	0.13	0.13	0.05
Redear sunfish	17	46.9 ± 11.7	Shallow	0.01	0.92	0.02	0.01	0.03	0.01
	30	40.1 ± 9.9	Intermediate	0.02	0.81	0.10	0.04	0.01	0.03
	7	34.0 ± 14.0	Deep	0.01	0.73	0.15	0.08	0.03	<0.01
Longear sunfish	15	128.4 ± 33.0	Shallow	0.01	0.70	0.11	0.08	0.09	0.01
	22	68.2 ± 9.6	Intermediate	0.02	0.41	0.20	0.07	0.26	0.04
	6	65.7 ± 12.7	Deep	0.01	0.38	0.39	0.10	0.07	0.05
Warmouth	1	4.0	Shallow		0.25	0.25	0.25	0.25	
	18	2.1 ± 0.8	Intermediate		0.18	0.34	0.08		0.40
	29	34.4 ± 9.2	Deep	0.52	0.04	0.10	0.24	0.02	0.08
Green sunfish	5	80.0 ± 62.6	Shallow		0.58	0.04	0.05	0.31	0.03
	3	11.7 ± 1.9	Intermediate		0.54	0.26	0.03	0.03	0.14
	0		Deep						

Prey distributions and/or differences in foraging ability greatly influenced sunfish diets in vegetated and nonvegetated habitats (Tables 36 and 37). Ostracods made up a greater proportion of the diets of most species in nonvegetated areas. In contrast, chydorids and chironomids were more important in the diets of fish collected from vegetated habitats. Detailed comparisons of diet of yoy sunfish from Lake Rush with similar studies in other areas are of limited value without knowledge of prey availability, and how different fish communities might partition or perhaps deplete various resources. However, the five major food items of yoy sunfish in Lake Rush were also the most common items in diets of small sunfish in other lakes (Larimore 1957; Applegate et al. 1967; Germann et al. 1975; Sadzikowski and Wallace 1976; Keast 1978b). The only major difference between these studies and mine is the much greater utilization of ostracods by sunfish in Lake Rush. I found only two other reports (Gerking 1962; Sadizkowski and Wallace 1976) of large numbers of ostracods in centrarchid diets.

Vinyard (1979) found that 26% of the ostracods consumed by small bluegills were expelled alive in the feces, and only 30% of those ingested showed major evidence of being digested. I did not attempt to quantify the number of ostracods in various stages of digestion; however, I often observed large numbers of whole ostracods in the intestines of many sunfish. Ostracods, because of their resistance to digestion, may have limited nutritional value. Their numerical importance in sunfish diets may well reflect the general paucity or vulnerability of other prey items in Lake Rush.

Table 36. Proportionate abundance of prey items in diets of yoy sunfish collected from vegetated and nonvegetated habitats in 1980.

Species	N	Mean number of prey/fish (± S.E.)	Vegetation	Proportion of diet					
				Daphnia	Ostracoda	Chironomidae	Copepoda	Chydoridae	Other
Bluegill	85	11.3 ± 2.1	Present	0.15	0.13	0.22	0.05	0.38	0.07
	5	53.0 ± 11.0	Absent	0.04	0.55	0.15	0.17	0.08	0.02
Redear sunfish	86	14.7 ± 2.9	Present	0.01	0.49	0.16	0.05	0.26	0.02
	11	32.5 ± 14.3	Absent	<0.01	0.99				
Longear sunfish	4	8.3 ± 6.3	Present		0.27	0.18		0.55	
	58	11.2 ± 1.8	Absent	0.01	0.66	0.12	0.02	0.18	0.01
Warmouth	67	5.4 ± 1.7	Present	0.12	0.37	0.34	0.11	0.01	0.04
	2	0.0	Absent						
Green sunfish	9	1.1 ± 0.5	Present		0.20	0.30			0.50
	1	21.0	Absent	0.81			0.14	0.05	

Table 37. Proportionate abundance of prey items in diets of yoy sunfish collected from vegetated and nonvegetated habitats in 1981.

Species	N	Mean number of prey/fish (± S.E.)	Vegetation	Proportion of diet					
				Daphnia	Ostracoda	Chironomidae	Copepoda	Chydoridae	Other
Bluegill	51	58.8 ± 10.2	Present	0.15	0.10	0.27	0.15	0.30	0.04
	11	68.0 ± 14.1	Absent	0.21	0.35	0.07	0.22	0.09	0.06
Redear sunfish	48	41.8 ± 7.4	Present	0.01	0.82	0.09	0.04	0.02	0.02
	6	38.7 ± 17.3	Absent		1.00				
Longear sunfish	18	58.5 ± 5.3	Present	0.01	0.35	0.29	0.11	0.17	0.07
	25	110.7 ± 21.5	Absent	0.01	0.63	0.13	0.07	0.15	0.01
Warmouth	42	22.5 ± 6.8	Present	0.53	0.04	0.12	0.21	0.02	0.08
	6	15.8 ± 8.4	Absent	0.17	0.12	0.06	0.49	0.03	0.13
Green sunfish	8	54.4 ± 39.5	Present		0.57	0.06	0.05	0.28	0.04
	0		Absent						

Feeding Periodicities

I used the average number of prey per stomach as a measure of foraging activity, and separated all fish into five time periods based upon the time of day traps were set. Because few green sunfish were examined and most were collected during the first and last time periods, they were excluded from this analysis. The remaining species of sunfish consumed high numbers of prey in mid-morning and late afternoon or evening (Figure 5). Foraging activity of bluegills and longear sunfish showed the greatest amplitude among all species. In all species,the fewest prey were found in fish collected in the middle of the day. Though prey numbers in warmouth stomachs were bimodal, more prey occurred in fish collected before 1200 h. Bluegills were the only species that fed mostly near dusk; the other sunfish consumed the most prey earlier in the evening. All fish used for food habits analysis were collected between 0600 and 2100 h; therefore, these data provide information only on daytime foraging activities.

Peaks in foraging activity agree quite well with fish activity (as measured by trap catches). However, peak numbers of bluegills were caught one time period before the peak in stomach contents. Since traps were set only on the substrate, this could indicate that movement of bluegills increased just prior to foraging, particularly if they moved up in the water column to forage. Alternatively, since stomach contents reflect previous feeding activity as well as digestive rates, the highest trap catches may correspond to the period of greatest foraging activity. Foraging activity of bluegills in the littoral zone appears to be somewhat size related (Baumann and Kitchell 1974). Young-of-year bluegills in Lake Rush had a feeding pattern similar to that reported by

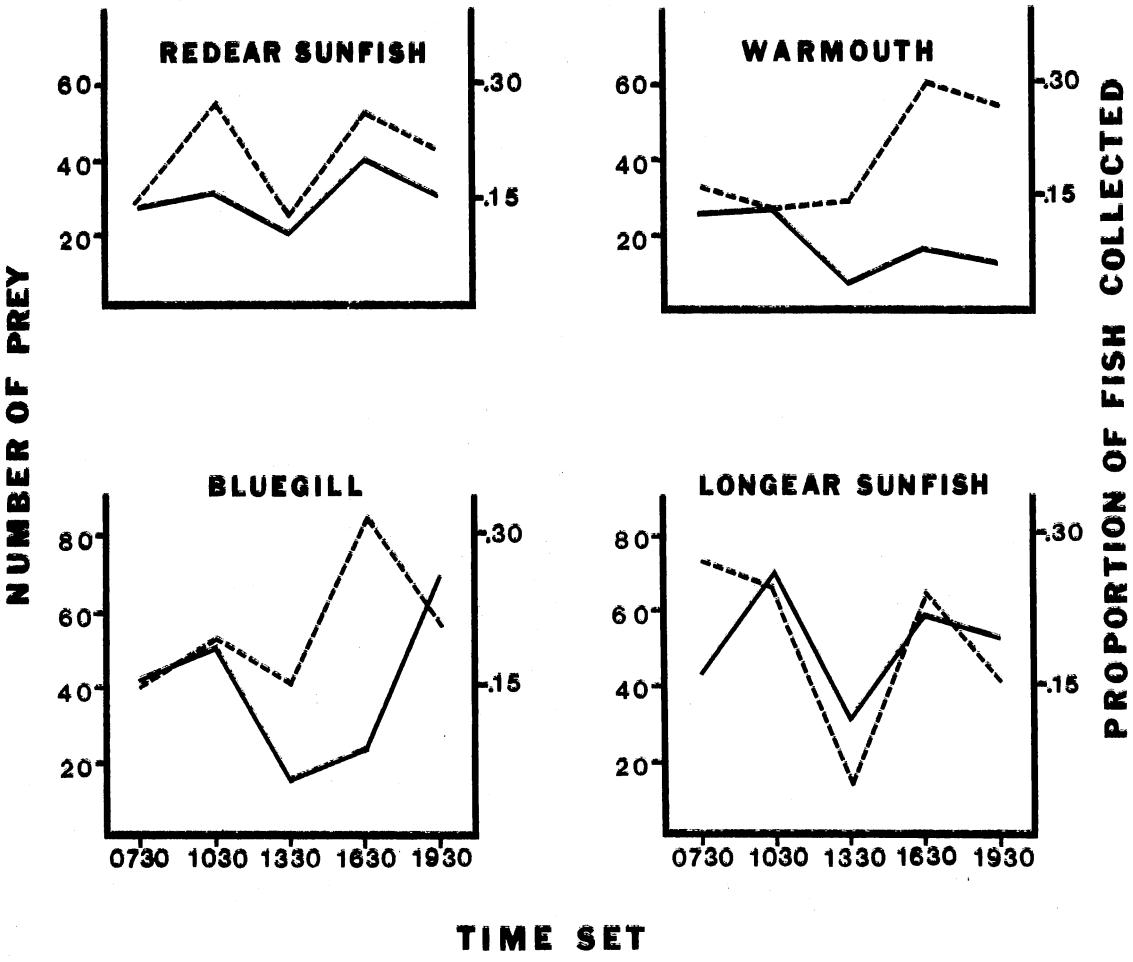

Figure 5. Mean number of prey items in sunfish stomachs (solid lines), and proportion (adjusted for trapping effort) of each species of sunfish collected in minnow traps over time of day (broken line).

Baumann and Kitchell (1974) for bluegills 75 to 95 mm TL (the smallest size they examined) collected from the littoral zone. In contrast, Keast and Welch (1968) reported peaks in feeding activity of bluegills at 1500 h and between 1830 and 2100 h.

Based on volume and condition of stomach contents, Larimore (1957) suggested that older warmouths feed in early morning, and possibly near dusk. However, he did not have nighttime samples. I also found maximum numbers of prey in warmouth collected in the morning, and there were indications of some feeding late in the day. In contrast to stomach contents, trap catches of warmouth indicate greatest activity late in the day. There are two possible interpretations of my data and Larimore's. The simplest is that activity level of warmouth (as determined by trap catches) is not associated with feeding. This seems unlikely, since both of these measures of activity agree well for the other species. It is more likely that the increase in warmouth activity late in the day coincides with the onset of foraging, and they feed either crepuscularly or throughout the night.

Prey Size

All species of sunfish ate prey of similar size (Figure 6), and differences between species in the shape of their utilization functions were simply a reflection of the type of prey consumed. For example, the average width of food items found in redear sunfish stomachs was 0.35 mm; ostracods which made up 60 to 84% of the redear sunfish diet each year, averaged 0.39 mm in width (Table 38).

Although most least squares regressions of either prey width or prey length on fish length were significant ($p < 0.05$), all regression

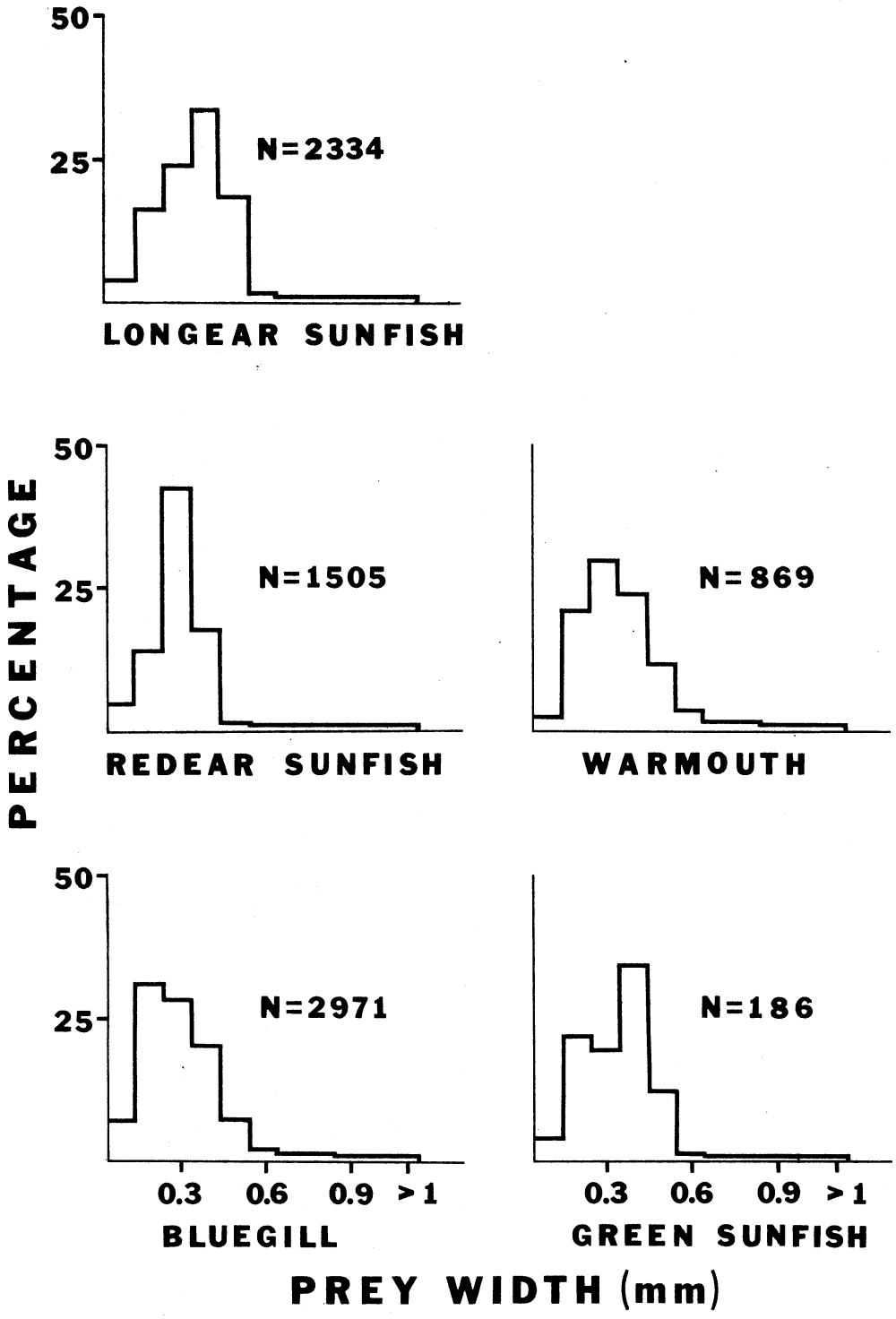

Figure 6. Frequency distributions for sizes of prey found in sunfish stomachs.

Table 38. Mean width and length of major prey consumed by yoy sunfish.

	Width			Length		
Prey	Mean	S.D	N	Mean	S.D.	N
Chironomidae	0.23	0.13	2023	1.89	0.83	207
Chydoridae	0.30	0.09	1166	0.65	0.14	107
Copepoda	0.30	0.10	1159	0.98	0.40	66
Daphnia	0.36	0.16	586	0.72	0.26	60
Ostracoda	0.39	0.07	2369	0.59	0.29	215

coefficients were less than 0.07 and the regressions never accounted for more than 15% of the variance in prey size. In a study of the diets of older sunfish in Lake Rush, prey size and fish length were more strongly related (Layzer and Clady unpublished data). The lack of any biologically meaningful relationship between prey size and fish length for yoy sunfish is likely a result of the small size range of fish examined (21 to 45 mm for bluegills), and the limited range of prey types and sizes consumed (Table 38).

Niche Breadth

Overall niche breadth values can be influenced by two factors: the number of observations and temporal shifts in resource usage. To determine if sample size affected my data, I plotted values of niche breadth for depth against catch per unit effort (CPUE) for each species for each sampling period that fish were collected (Figure 7). For the rarer species, warmouth and longear sunfish, niche breadth was highly variable for similar densities. In contrast, niche breadth for the dominant species (bluegills and redear sunfish) was surprisingly similar within years for CPUE > 0.1. At lower densities, too few observations were available to determine if niche breadth for bluegills and redear sunfish was as variable as it was for the rarer species. Plots of niche breadth for depth against sampling dates would be nearly identical to the plots of niche breadth against CPUE for bluegills for both years and for redear sunfish in 1981 (see Tables 5 and 6 for CPUE over time). Because only two resource states were used in calculating niche breadth for vegetation, the possible values that this variable could have were limited in range (.5 to 1.0). Partly as a result of this limited range,

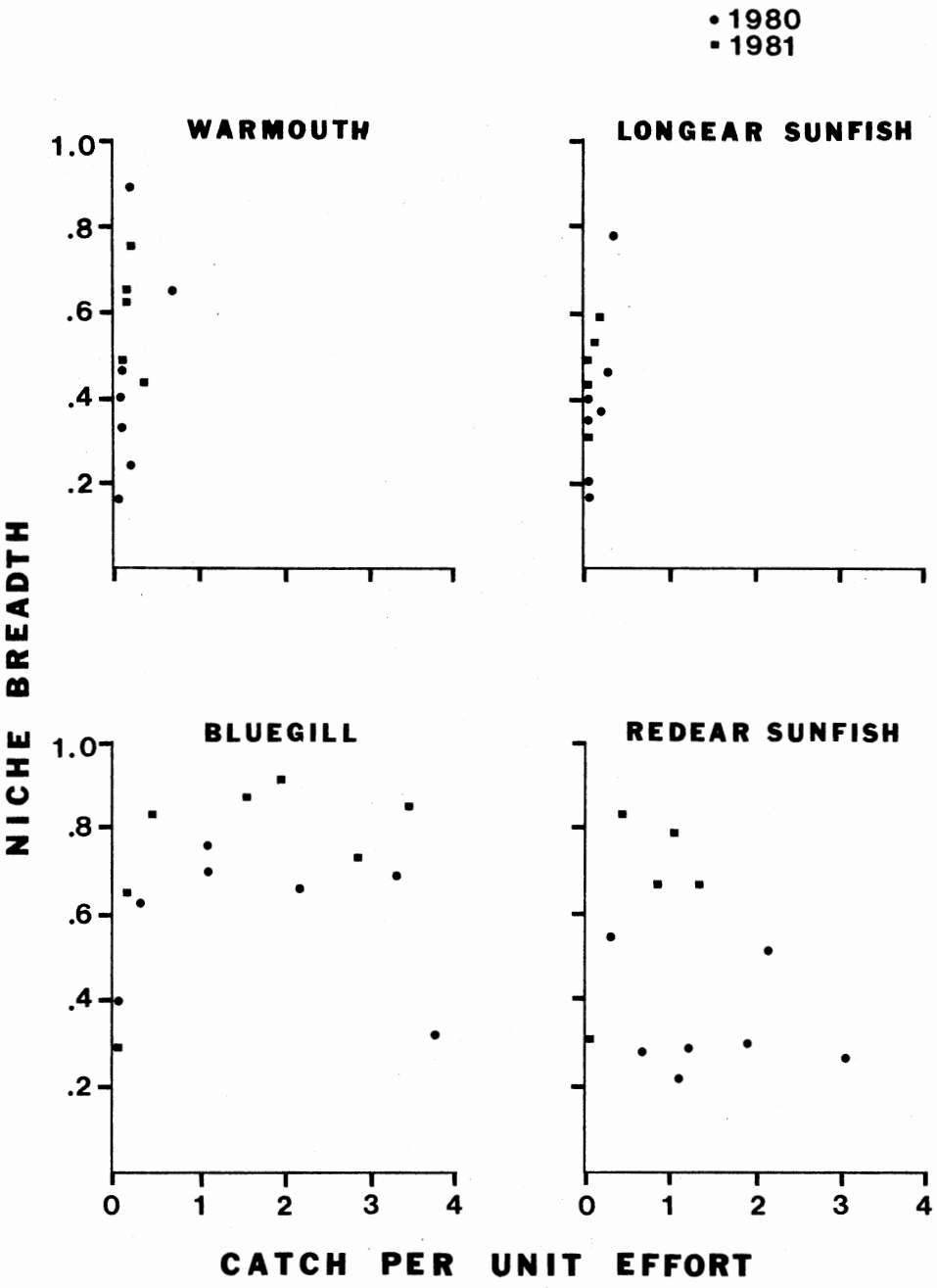

Figure 7. Niche breadth for depth and catch per unit effort for each species of sunfish. Points represent each sampling period that fish were collected.

each species' niche breadth for vegetation varied little (maximum difference of .14) between sampling periods with no observable trend. Because there was little variation in niche breadth for depth within years for the abundant species, and because there was minimal variation in vegetation usage by all species, niche breadth for yoy sunfish in Lake Rush is best estimated by combining data within years.

Except for the use of vegetation in 1981, bluegills had the broadest niches for all resource sets (Table 39). Compared to 1980, all species were more evenly distributed over depth in 1981 when niches of sunfish shifted towards deeper water (Figure 3 and Table 39). This change in depth usage was most striking for redear sunfish; their niche breadth for depth increased from .29 to .80. In 1981, niche breadth of bluegills for depth approached 1.0, indicating a nearly uniform distribution over the depth range sampled. Only bluegills were more restricted in their usage of vegetated and nonvegetated habitats in 1981 compared to 1980; all other species were more evenly distributed between the two resource states. The increase in niche breadth of longear sunfish for vegetation reflects their substantially greater usage of vegetated habitats in 1981. Similarly, the slight decrease in niche breadth of bluegills resulted from a greater use of vegetated areas in 1981. The increases, though slight, in niche breadth for vegetation of other species in 1981, were due to increased use of nonvegetated habitats.

Unlike the consistent increases observed in niche breadth values for the habitat dimensions, changes in relative use of prey types showed no trend across species between years. Interestingly, the proportional usage of the various prey types by redear sunfish changed the most of

Table 39. Niche breadth of yoy sunfish for habitat and diet.

Year	Resource set	Species				
		Bluegill	Redear sunfish	Longear sunfish	Warmouth	Green sunfish
1980	Depth	.71	.29	.41	.60	.17
1981	Depth	.94	.80	.62	.68	.59
1980	Vegetation	.80	.61	.53	.60	.50
1981	Vegetation	.71	.72	.85	.66	.83
1980	Prey type	.78	.39	.39	.59	.48
1981	Prey type	.86	.23	.49	.51	.40

any species between years; however, this change was in precisely the opposite direction of the changes noted in their relative usage of habitats. Apparently, redear sunfish foraged over a greater range of habitats in 1981, but became more restrictive in their feeding (recall Tables 34 through 37). Proportional resource usage by warmouths was the most stable observed for any species; for all resource sets, changes in the proportionality in their resource use between years were minimal.

Niche Overlap

Overlap values for use of vegetation between longear sunfish and each of the other species were exceedingly low (all $< .30$) in 1980 (Table 40). In contrast, overlap values for use of vegetation between all other pairs of species were among the highest for any niche axis (all $\geq .75$). A similar pattern existed in 1981 (Table 41), except that overlaps between longear sunfish and other species increased. Nevertheless, vegetation overlap values between longear sunfish and all other species were only about one half the size of overlaps between other species pairs. In 1980, overlap in depth utilization was moderately high (.55 to .75) for many species pairs. Depth overlap increased in 1981 for most species comparisons, indicating a greater similarity in depth distribution.

There was strong complimentarity between the use of vegetation and depth in 1980. Seven of the ten species pairs overlapped greatly along one habitat axis but little on the other. For example, redear sunfish and warmouth had identical distributions along the vegetation dimension ($O = .99$), but overlapped little (.34) in their depth distribution. Spatial segregation was less obvious in 1981, partially as a result of

Table 40. Proportional overlap between each species pair for all resource sets for 1980. Sample sizes (habitat/prey): bluegills (853/90); redear sunfish (839/97); longear sunfish (75/62); warmouth (82/69); green sunfish (8/10).

Species pair	Resource set			
	Vegetation[1]	Depth	Habitat[2]	Prey type
Bluegill - Redear sunfish	.85	.61	.52	.62
Bluegill - Longear sunfish	.28	.62	.17	.58
Bluegill - Warmouth	.84	.66	.55	.67
Bluegill - Green sunfish	.75	.36	.27	.43
Redear sunfish - Longear sunfish	.13	.74	.10	.96
Redear sunfish - Warmouth	.99	.34	.34	.57
Redear sunfish - Green sunfish	.90	.75	.68	.25
Longear sunfish - Warmouth	.12	.33	.04	.54
Longear sunfish - Green sunfish	.03	.55	.02	.23
Warmouth - Green sunfish	.91	.09	.08	.41

[1] Vegetation dimension has two resource states: presence or absence of vegetation.

[2] Product of overlap values for vegetation and depth.

Table 41. Proportional overlap between each species pair for all resource sets for 1981. Sample sizes (habitat/prey): bluegills (1074/62); redear sunfish (381/54); longear sunfish (62/43); warmouth (100/48); green sunfish (5/8).

Species pair	Resource set			
	Vegetation[1]	Depth	Habitat[2]	Prey type
Bluegill - Redear sunfish	.99	.73	.72	.31
Bluegill - Longear sunfish	.47	.73	.34	.60
Bluegill - Warmouth	.96	.64	.61	.52
Bluegill - Green sunfish	.91	.62	.56	.53
Redear sunfish - Longear sunfish	.48	.71	.34	.71
Redear sunfish - Warmouth	.95	.46	.44	.20
Redear sunfish - Green sunfish	.92	.82	.75	.69
Longear sunfish - Warmouth	.43	.46	.20	.28
Longear sunfish - Green sunfish	.56	.66	.37	.82
Warmouth - Green sunfish	.87	.29	.25	.19

[1] Vegetation dimension has two resource states: presence or absence of vegetation.

[2] Product of overlap values for vegetation and depth.

increases in depth overlap among most species pairs and the increased usage of vegetation by longear sunfish.

Since the presence or absence of vegetation was independent of the depth range sampled, I multiplied overlap values for these two dimensions to obtain the best estimate of overall habitat overlap (May 1975). These estimates reflect the strength of the complimentarity in the use of depth and vegetation: habitat overlap was minimal for most species in 1980, but uniformly increased in 1981.

Longear sunfish and redear sunfish had nearly identical diets in 1980 (Table 40). Although their diets diverged somewhat in 1981, overlap was still high (Table 41). Most other species showed more substantial changes in diet overlap between years. For example, overlap between redear sunfish and bluegills decreased from .71 in 1980, to .31 in 1981. While most species were separated to a greater degree spatially in 1980 compared to 1981, diet overlaps indicated that food was more important in segregating species in 1981.

Because sunfish diets differed with respect to presence or absence of vegetation and at different depths, I also calculated separate diet overlap values (partitioned overlaps) for fish within each habitat category. Between years there was no consistent relationship between the overall diet overlap and partitioned overlap values for each species pair for vegetated and nonvegetated habitats (Tables 42 and 43). In 1980 however, partitioned overlap values were generally lower than the combined diet overlap values for most species pairs, suggesting that real niche overlap may be lower than estimated. In 1981, there was little difference between partitioned overlap values and the overall diet overlap. A similar relationship existed between overall diet

Table 42. Partitioned overlap values between each species pair for prey type for 1980. Separate overlap values were calculated for fish collected in vegetated and nonvegetated habitats. Sample sizes (vegetation, present/absent): bluegills (85/5); redear sunfish (86/11); longear sunfish (4/58); warmouth (67/2); green sunfish (9/1).

Species pair	Vegetation		Arithmetic average	Overall*
	Present	Absent		
Bluegill - Redear sunfish	.63	.56	.60	.62
Bluegill - Longear sunfish	.81	.79	.80	.58
Bluegill - Warmouth	.57			.67
Bluegill - Green sunfish	.42	.23	.33	.43
Redear sunfish - Longear sunfish	.71	.67	.69	.96
Redear sunfish - Warmouth	.62			.57
Redear sunfish - Green sunfish	.38	.01	.20	.25
Longear sunfish - Warmouth	.46			.54
Longear sunfish - Green sunfish	.38	.08	.23	.23
Warmouth - Green sunfish	.54			.41

*Calculated as in Tables 40 and 41;

Table 43. Partitioned overlap values between each species pair for prey type for 1981. Separate overlap values were calculated for fish collected in vegetated and nonvegetated habitats. Sample sizes (vegetation, present/absent): bluegills (51/11); redear sunfish (48/6); longear sunfish (18/25); warmouth (42/6); green sunfish (8/0).

Species pair	Vegetation		Arithmetic average	Overall*
	Present	Absent		
Bluegill - Redear sunfish	.28	.35	.32	.31
Bluegill - Longear sunfish	.70	.60	.65	.60
Bluegill - Warmouth	.52	.66	.59	.52
Bluegill - Green sunfish	.53			.53
Redear sunfish - Longear sunfish	.53	.64	.59	.71
Redear sunfish - Warmouth	.22	.12	.17	.20
Redear sunfish - Green sunfish	.71			.69
Longear sunfish - Warmouth	.37	.30	.34	.28
Longear sunfish - Green sunfish	.67			.82
Warmouth - Green sunfish	.21			.19

*Calculated as in Tables 40 and 41;

overlaps and diet overlaps partitioned by depth: in 1980 the overall diet overlap was generally greater than the partitioned values, and in 1981 there was little difference (Tables 44 and 45). Perhaps because the general diet overlap values for all species pairs (excluding green sunfish) decreased in 1981, further diet separation within habitats was precluded.

If congeneric species are potentially strong competitors, they should compliment each other strongly in resource usage if resources are in fact limited. This is precisely what some of the yoy sunfish in Lake Rush did. The few observations of green sunfish do not allow discussion of overlap between them and other species. In 1980, all other species pairs had relatively high dietary overlaps with low to moderate overlap for habitat. Longear sunfish and redear sunfish showed the greatest complimentarity; these two species had the greatest overlap value of any species comparisons for prey type, but their overlap in space was among the lowest. Niche complimentarity was also evident in 1981; even though habitat overlap increased between most species, it was often accompanied by a substantial decrease in diet overlap. However for some pairs of species, complimentarity of niche dimensions was not evident. For example, longear sunfish and warmouth segregated both by habitat and diet in 1981.

The complementarity between species in their use of habitat and food, and the shift in relative importance of these two dimensions for segregating species suggests that a combination of these two dimensions would provide the best estimate of overall niche overlap. From the preceding documentation of dietary differences among fish collected at different depths and in the presence or absence of vegetation, it is

Table 44. Partitioned overlap values between each species pair for prey type for 1980. Separate overlap values were calculated for fish collected at different depths. Depth categories are as in Tables 34 and 35. Sample sizes (depth, shallow/intermediate/deep): bluegills (56/30/4); redear sunfish (78/18/1); longear sunfish (44/18/0); warmouth (23/25/21); green sunfish (10/0/0).

Species pair	Depth category			
	Shallow	Intermediate	Deep	Overall*
Bluegill - Redear sunfish	.65	.38	.46	.62
Bluegill - Longear sunfish	.62	.38		.58
Bluegill - Warmouth	.50	.71	.56	.67
Bluegill - Green sunfish	.36			.43
Redear sunfish - Longear sunfish	.98	.95		.96
Redear sunfish - Warmouth	.78	.32	.15	.57
Redear sunfish - Green sunfish	.26			.25
Longear sunfish - Warmouth	.79	.27		.54
Longear sunfish - Green sunfish	.24			.23
Warmouth - Green sunfish	.37			.41

*Calculated as in Tables 40 and 41;

Table 45. Partitioned overlap values between each species pair for prey type for 1981. Separate overlap values were calculated for fish collected at different depths. Depth categories are as in Tables 34 and 35. Sample sizes (depth, shallow/intermediate/deep): bluegills (19/30/13); redear sunfish (17/30/7); longear sunfish (15/22/6); warmouth (1/18/29); green sunfish (5/3/0).

Species pair	Depth category			
	Shallow	Intermediate	Deep	Overall*
Bluegill - Redear sunfish	.22	.30	.58	.31
Bluegill - Longear sunfish	.45	.69	.75	.60
Bluegill - Warmouth	.71	.47	.51	.52
Bluegill - Green sunfish	.58	.47		.53
Redear sunfish - Longear sunfish	.78	.61	.66	.71
Redear sunfish - Warmouth	.31	.35	.26	.20
Redear sunfish - Green sunfish	.65	.71		.69
Longear sunfish - Warmouth	.53	.49	.32	.28
Longear sunfish - Green sunfish	.77	.71		.82
Warmouth - Green sunfish	.59	.61		.19

*Calculated as in Tables 40 and 41;

apparent that diet and habitat are not independent. However, because most species consumed the same array of prey items, though in different proportions, it is obvious that these two dimensions are at least partially independent. As a conservative estimate (biased upwards), I used the arithmetic average of the diet and habitat overlaps to obtain an estimate of niche overlap for each species pair. Arithmetic averages are most appropriate when dimensions are totally dependent, in which case they provide the best estimate of niche overlap (May 1975). Therefore in cases of partial independence, the arithmetic average overestimates true niche overlap. Nevertheless, it is still informative to compare these average niche overlap values between years. Because of sample size, overlap values between green sunfish and other species probably are not accurate and therefore will not be discussed. Given the greater dependence of diet and habitat in 1980, it is rather surprising that niche overlaps are quite similar between years (Figure 8). Maximum difference in niche overlap between years was .14. Interestingly, overlap between longear sunfish and redear sunfish was identical between years. These are the two species that showed the greatest degree of complimentarity in their use of food and habitat. Furthermore, redear showed the greatest increase in niche breadth for depth, and longear sunfish showed the greatest increase in niche breadth for vegetation. Since niche overlap varied little between years for each pair of species, it is not surprising that the average niche overlap among the sunfish community changed only slightly between years (.49 to .44).

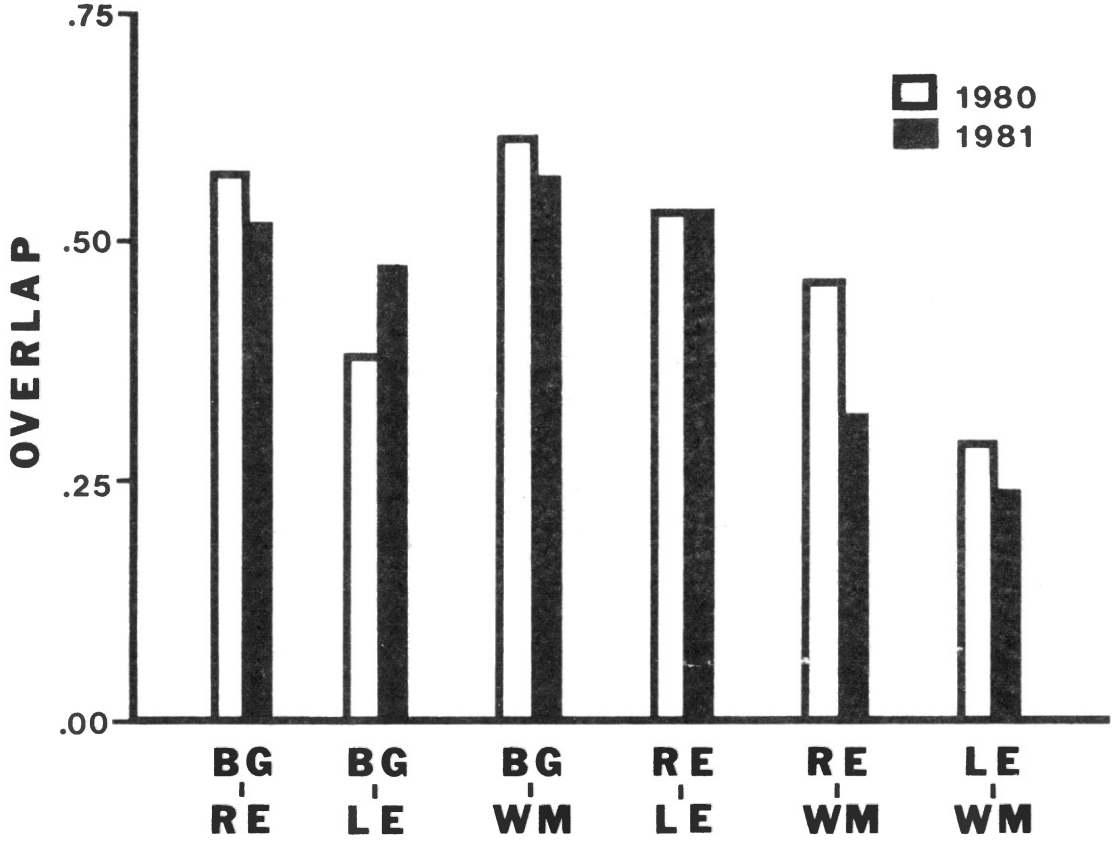

Figure 8. Average niche overlap among four species of sunfish (open bars, 1980; solid bars, 1981). BG = bluegill; RE = redear sunfish; LE = longear sunfish; WM = warmouth.

CHAPTER V

DISCUSSION

Contrary to my preliminary observations, coexisting yoy sunfish in Lake Rush were ecologically segregated to a remarkable degree. In 1980, longears were clearly separated from other congeners by their extensive use of nonvegetated habitats. While the presence or absence of vegetation was still very important for isolating longears in 1981, depth was also important. Together these two habitat dimensions effectively separated longears from other sunfish species. The remaining four species of sunfish lived primarily in vegetated areas. Other researchers have also found that small sunfish were restricted to dense vegetation (Hall and Werner 1977; Keast 1978a; Werner et al. 1977), where it is generally assumed that the risk of predation is lower.

If predation restricts the habitat choices by prey, then the increased density in vegetated areas must raise the level of potential competition. Mittlebach (1981b) developed an optimal foraging model based on laboratory experiments with bluegills. Field tests of this model showed good agreement between fluctuations in resource abundance in different habitats, and shifts in habitat use (and correspondingly the diet) of large bluegills. However, even though he demonstrated that small bluegills could increase their energetic intake by leaving the vegetation and foraging in other habitats, they remained in the

vegetation. He concluded that the risk of predation restricted bluegills to dense vegetation. He further suggested that, as a result of the risk to predation, yoy sunfish that are restricted to the vegetation may be incapable of partitioning resources, since their morphology may be better adapted to later life stages. As a result competition could be intense if resources are limiting in the vegetation.

The density of yoy sunfish and their poor growth rates indicate that resources were in fact limiting in the vegetated areas of Lake Rush and that competition was imminent. Competition theory predicts two scenarios for such a situation: competitive exclusion if resources remain limiting, or partitioning of resources. I found substantial evidence of the latter. Species inhabiting the vegetation segregated both by depth and diet. Furthermore, the importance of these two dimensions changed between years, indicating a high level of behavioral plasticity for these species. In both years, depth was very important for separating redears and warmouths. Their distributions over depth were essentially mirror images; redears were most abundant in the shallowest areas, and warmouths were more abundant in the deepest areas. In 1980, overlap between bluegills and redears were moderately high (.61 and .62) for both depth and prey type. However, diet overlaps partitioned by depth or by the presence and absence of vegetation were reduced. This indicates that diets of these species diverged more when they occurred in the same habitats. In 1981, bluegills and redears were distinctly separated on the basis of diet even though their use of habitat was more similar. Clearly, coexistence of bluegills and redears was facilitated by feeding on different items while foraging the same

habitats.

It is more difficult to account for the moderately high overlap between bluegills and warmouths for both habitat and diet. Even when diets were partitioned by habitat categories, little additional separation occurred. This anomaly might be explained in a number of ways. The observed overlap values might approximate the maximum tolerable overlap between these species (Pianka 1972); consequently, the observed level of resource partitioning was sufficient to allow coexistence. Alternatively, these two species may have segregated along an additional dimension or by a finer resolution of microhabitat than I recognized, which is suggested by the warmouths' preference ($p < 0.001$) of dense versus sparse stands of Ceratophyllum while bluegills showed no such preference. There is also the possibility that the time dimension was important in separating these species. The fewer prey found in warmouth stomachs, and their general activity pattern suggests that warmouths may have increased foraging near or after dark; if so, they may have foraged in different habitats or on items not generally found in their stomachs during the day. Similarly, bluegills and warmouths could have foraged in different levels of the water column. Differences in foraging level have frequently been cited as mechanisms for segregating stream fishes (Mendelson 1975; Smart and Gee 1979; Baker and Ross 1981). However, if the same prey base was used (and many of their food items do undergo a vertical migration), then differences in foraging level would not be effective in separating these species. Moreover, if the prey base differed with respect to height in the water column, this difference should have been reflected in stomach contents.

Given Vinyard's (1979) observation that only 30% of the ostracods

ingested by bluegills were digested, a perplexing question remains: "Why were ostracods so common in the diets of all sunfish?". It is difficult to answer this question without knowledge of abundance, distribution, and relative vulnerability of other prey in Lake Rush. Because of their apparently low nutritional value, it is unlikely that ostracods were a preferred food item; yet they made up 84% of the redear diet. I suggest that if yoy sunfish are competing for food it is based on the quality and not the quantity of food items. The density of prey with poor nutritional value, such as ostracods, may be high enough so that sunfish are able to meet their basic metabolic demands with minimal amounts of energy being available for growth. Viewed in this light, foraging in temperate lakes on nutritionally poor prey may be a survival strategy until the following spring, when typically there is an abundance of food (Mittlebach 1981a). Further, volume of stomach contents is greatest in the spring (Seaburg and Moyle 1964), and spring is the period of greatest growth for most species (see Carlander 1969; 1977; for general review).

An additional mechanism which may have helped to reduce interspecific competition among sunfish in Lake Rush is differences in spawning seasons. Temporal segregation of yoy fish appears to be important among other genera, especially those inhabiting cold water streams (Everest and Chapman 1972; Gibbons and Gee 1972; Williams 1981). Intergeneric differences in peaks of larval abundance have been reported for temperate lakes and are probably important in reducing competition early in life (Faber 1967; Amundrud et al. 1974). In lepomids, there is great intraspecific variability in time of spawning and generally broad overlap among species. For instance, bluegills have been observed

spawning from April through October in Alabama (Swingle and Smith 1943), in other areas their spawning seasons are more restricted (Morgan 1951; Cross 1967; Cohen and Brown 1969). Spawning seasons of other sunfish are also variable, but are generally shorter than the bluegill's (Cross 1967; Miller and Robison 1973; Pfleiger 1975).

Incidental observations of sunfish spawning in Lake Rush are insufficient to precisely define sunfish spawning, and may be biased because of differences in relative abundance of species. Also, water transparency limited these observations to depths of about 1 m or less. In 1981, male bluegills and redear sunfish were first observed guarding nests early in April. Spawning of redear sunfish appeared to be completed by early July, while some bluegills were still guarding nests until early August. In 1980, observations were not made until early May when bluegills and redear sunfish were already nesting. Longear sunfish and green sunfish were seen on nests only during May and June of each year. No warmouth nesting activity was observed. Both the catches of yoy in minnow traps and the length frequency distributions of yoy for each species suggest that my observations of relative nesting activity between species is reasonably accurate.

In both years, bluegill abundance was correlated with collection date (Spearman's rho $\geq$ .93, $p < 0.025$). The consistent, and often significantly, smaller average size of bluegills compared to the other species also was the result of continued recruitment of bluegills to the sampling gear; presumably these recruits were produced by late-spawning fish. Although nesting redear sunfish were observed early in April, the drop in water temperature or perhaps the herbicide application, seriously limited reproductive success. By May they had returned to the

nesting area. Wilbur (1969) noted that a similar decrease in water temperature interrupted redear sunfish spawning for about two weeks. Trap catches indicated that successful reproduction of redear sunfish occurred later in 1981 than in 1980.

It is often assumed that fish hatched later in the summer have a lower overwinter survival rate because of their small size at the end of the growing season. However, Larimore (1957) indicated that even though later broods of warmouths are faced with a greater number of predators, their survival is often greater because macrophyte density reduces their vulnerability to predation. After conducting experiments and reviewing other studies, Toneys and Coble (1979) concluded that there was no clear relationship between size and overwinter survival.

If overwinter survival is unrelated to size, the bluegill's strategy of a protracted spawning season may increase their fitness. Moreover, bluegills spend the first six or seven weeks of their life in the limnetic zone (Werner 1969). Use of the relatively large limnetic zone should reduce competitive interactions with congeners and larger yoy conspecifics inhabiting the littoral zone. The numerical dominance of bluegills in Lake Rush and other waters may in part be related to their long reproductive season and their ability to exploit the limnetic zone, both as larvae and later as adults. Svardson (1976) indicated that numerically dominant species are typically those that can utilize the zooplankton resource of the limnetic zone.

Use of exposed habitats in Lake Rush by yoy longears is in sharp contrast to their spatial distribution in Michigan lakes (Laughlin and Werner 1980). In Michigan lakes, small longear were largely confined to dense vegetation along with small pumpkinseeds (L. gibbosus); however,

Laughlin and Werner (1980) noted that larger longears lived primarily in sparsely vegetated areas, though they were infrequently encountered in areas of no vegetation. Among the many possible explanations for these observed differences in habitat utilization among lakes, I believe the following merit consideration. Subspecific taxonomy of longears is unclear and currently is being studied (Bauer 1978); hence it is possible that longears in Lake Rush and Michigan are different subspecies. Even if they are the same subspecies, phenotypic differences may simply reflect differences in populations which are adapted to local conditions. An alternative explanation is that the observed differences reflect community composition, specifically within the genus Lepomis. The changes in depth distribution of longears in 1981 indicates that the explanation for their distribution in vegetated and nonvegetated habitats is complex.

The interpretation and understanding of resource use by yoy sunfish in Lake Rush is greatly facilitated by two fortuitous events in 1981: the profound change in the aquatic macrophyte community resulting from the herbicide application, and the substantial overall reduction in abundance of redear sunfish. I suggest that increased usage of vegetated habitats by longears in 1981 was related both to the decrease in relative abundance of redears and to changes in the macrophyte community. In 1980, all species avoided Myriophyllum over a depth range of 50 to 200 cm, and longears were extremely rare in traps set in the vegetation. With the change in plant species in 1981, all species made greater use of deeper water. Longears collected in vegetated areas in 1981, were most common at depths > 100 cm. Apparently, Chara and Ceratophyllum provided a greater return to foraging longears in 1981

compared to fish foraging in Myriophyllum in 1980. The differences in depth distribution of redears and longears in 1981, and more importantly, the greater shift towards deeper water by longears suggests longears may have been avoiding areas of greatest redear abundance. Furthermore, longears also increased the breadth of their diet in 1981, while redears restricted their diet, thus reducing niche overlap.

In 1980, longears were apparently subjected to a greater risk of predation since they lived almost exclusively in nonvegetated areas. In 1981, reduced abundance of redears, and changes in the composition of the plant community may have increased the expectation of yield from vegetated habitats. Since both predation and competition are negative interactions, I suggest that in 1980 longears adopted the strategy of incurring a greater risk of predation to minimize the effects of competitive interactions. If longears were inferior competitors in the vegetation as I suggest, then the low abundance of this species in Lake Rush may have been directly linked to their higher risk of predation in nonvegetated areas. Although Werner and Hall (1977) have convincingly demonstrated niche shifts for lepomids in the presence of a superior competitor under controlled conditions, it is dangerous to invoke competition as the driving force behind niche shifts observed in Lake Rush without performing controlled experiments.

Mechanisms underlying patterns of resource partitioning and apparent niche shifts in the field are usually not obvious. Andrusak and Northcote (1971) found different patterns of resource use among allopatric and sympatric populations of cutthroat trout (Salmo clarki) and Dolly Varden (Salvelinus malma). In the sympatric populations, the species were spatially segregated and consequently foraged on different

items. However, Schutz and Northcote (1972) demonstrated in laboratory experiments that individuals from the sympatric populations did not undergo niche shifts when maintained allopatrically. They concluded that the pattern of resource partitioning observed in the field was more likely the result of innate behavioral and morphological differences between the species. Pianka (1976) argued that species (and presumably populations) under continuous and intense competitive pressures may not undergo niche shifts when the competitor is removed. Thus, the behavioral plasticity observed between years in Lake Rush suggests that sunfish may not be subjected to continuous and intense competitive pressure. In fact, resources for which sunfish compete are likely to be variable and limiting over a relatively short period of time. Much ecological theory has been generated from studies of terrestrial organisms (MacArthur 1958; 1972; Pianka 1973; Roughgarden 1974). Metabolic constraints of endotherms in particular, but also many ectotherms, impose severe limits on the repertoire of responses to low levels of resource availability that terrestrial organisms may have. In contrast, the indeterminant growth rates of fish, and their ability to behaviorally alter metabolic rates in response to reduced food intake (Stuntz and Magnuson 1976), implies that they can greatly mediate the effects of competitive interactions, at least over the short term.

It seems likely that the coexistence of sunfish in Lake Rush is the result of a multitude of underlying factors, only some of which have been addressed in this study. Evolutionary history has set limits on the range of options available for resource exploitation by sunfish. Within this evolutionary framework, theory predicts optimal patterns of resource exploitation. In Lake Rush, it is evident that the observed

patterns of resource use by yoy sunfish reflect not only their evolutionary past, but also their integrated response to abiotic factors, competition, predation, and resource availability.

CHAPTER VI

PHENOTYPIC VARIATION IN YOUNG-OF-YEAR BLUEGILLS

Introduction

A broad niche, such as that observed for yoy bluegills in Lake Rush, can be achieved by populations in which individuals behave either as generalists exploiting the same broad array of resources, or as specialists utilizing narrow, but different ranges of resources (Roughgarden 1972; 1974). Phenotypically-expressed genetic variation can be maintained in a population by a variety of mechanisms. In his benchmark paper, Levene (1953) proposed a simple model for the maintenance of polymorphism in a panmictic population which occupies a patchy environment. Levene assumed that offspring randomly dispersed to different habitats where selection occurred and that selection favored different phenotypes in each habitat. He further suggested that genetic variability could be maintained more easily if individuals preferentially selected habitats where they were most fit.

Phenotypic variation in fish populations is common. Maintenance of intrapopulational (I use the term loosely here) variation in spawning location often can be explained on the basis of selection and reproductive isolation (Raleigh 1967; 1971; Northcote *et al.* 1970). Genetic differences which in themselves are adaptive may also be associated with such cases of reproductive isolation (Northcote and Kelso 1981). Growth rate is one highly variable characteristic both

within and between populations. Transfer experiments have indicated that the environment is often the most significant factor in determining growth rates (Rupp and Redmond 1966); yet selective breeding has also been successful in substantially increasing growth rate (Donaldson and Olson 1955; Donaldson and Menasveta 1961), thus demonstrating the influence of genotype on growth rate. Similarly, the influence of genotype and environment on morphological characteristics has been well established (Martin 1949; Harrington and Crossman 1976; and others).

In light of the demonstrated influence of both genotype and environment on phenotypic characteristics, it is not surprising that distinct polymorphism is rarely observed in fish populations. However, Allendorf et al. (1976) presented both electrophoretic and morphological evidence for the existence of two genetically isolated, sympatric populations of brown trout (Salmo trutta), though the underlying mechanism for this isolation is unknown. More often, phenotypic characteristics are generally distributed along a continuum with much variation within a population. Such variation may allow for a greater diversity in resource use by a population.

Because observations of an individual's use of resources is usually an instantaneous measure, it is difficult to assess the relative magnitude of the within and the between phenotypic components of niche breadth unless recognizably different phenotypes are encountered. Estimates of variability in resource use among individuals can be obtained by repeatedly recapturing marked individuals (Bryan and Larkin 1972). Where it is impractical to either mark or recapture a sufficient number of individuals, an alternative approach for estimating the importance of between phenotypic component, though not unequivocal, is

to determine if morphological variability is greater among (rather than within) resource states such as habitats. Greater morphological variability among resource states implies a rather significant between phenotypic component. I observed considerable variation in body form of yoy bluegills collected from Lake Rush; they also had broad niches (see Chapter IV). Objectives of this portion of my study were to: (1) determine if different morphological phenotypes of bluegills were associated with particular habitats in Lake Rush; (2) determine if fitness (as measured by growth rate) varied between habitats; (3) determine if selection occurred on meristic characters.

CHAPTER VII

MATERIALS AND METHODS

Morphology

Meristic counts and morphometric measurements were made on a total of 967 bluegills from more than four year classes collected by several methods over a three year period (Table 46). Fish were preserved and stored in 10% formalin, and counts and measurements were made three to four months later. For analysis, I selected eight meristic and metric characters that could be easily and accurately counted or measured on small fish (< 35 mm). Using dial calipers, the following characters for yoy fish were measured to the nearest 0.05 mm: body depth, caudal peduncle depth, head length, and standard length. Dorsal spines, soft dorsal and soft anal fin rays, and lateral line scales were counted under a dissecting microscope. All measurements and meristic counts follow Hubbs and Lagler (1970), except that body depth was measured along a line originating at the anterior base of the dorsal fin and running perpendicular to the midline of the fish.

Age Determination

All fish used for age and growth analysis were collected by minnow traps, placed in plastic bags, packed on ice, and frozen within 3 hours of collection. Prior to removing otoliths, meristic counts were made on these fish. Both sagitta were removed from each bluegill under a

Table 46. Collection dates and gear, sample sizes, age groups, and year classes of bluegills used for analysis of meristic and metric measurements.

Year	Month	Gear	N	Age group	Year class
1979	September	Seine	50	0+	1979
1980	July	Seine	25	0+	1980
1980	August - October	Traps	243	0+	1980
1980	October	Electrofishing	50	0+	1980
1980	October	Electrofishing	20	I+	1979
1981	May	Electrofising	77	I+	1980
1981	July - September	Traps	437	0+	1981
1981	June - August	Angling	40	$\geq$IV+	$\leq$1977
		Total	967		

dissecting microscope and mounted on separate glass slides with Canada balsam. Methods of otolith preparation were similar to those of Taubert and Coble (1977). Sagittal sections were prepared by alternately grinding the distal and proximate surfaces until the nucleus was evident when examined under a microscope. Mounted otoliths were ground by hand against a second glass slide covered with a mixture of water and silicon carbide (600 grit). The section was then etched with 1% HCl for 15 to 30 seconds. Otoliths were examined with a microscope at a magnification of 600X. Most often, the grinding and etching process had to be repeated one or more times before the nucleus and/or all rings could be observed. In many cases, repeated grinding of the otoliths failed to produce sections with easily discernable daily rings; visibility of rings on these otoliths was greatly enhanced by applying a drop of clearing agent (euparal). However even after clearing, both otoliths from 14% of the fish had to be discarded because I could not observe either the nucleus or any area of the otolith section in which all rings were present.

In addition to daily rings, Taubert and Coble (1977) indicated that subdaily rings are also present in otoliths of bluegills, and that these subdaily rings were more easily observed in frontal sections compared to sagittal sections. Occasionally, I observed subdaily rings on sagittal sections but they were not as well defined as daily rings. To determine the age of bluegills, I made two counts of all distinct rings present in the otoliths; if these counts differed by two or less, I used their average as an estimate of age. When the counts differed by more then two (23% of the otoliths) I made a third count and used the average of all three to estimate age. Most otoliths that were counted three times

contained 85 or more rings, and the maximum range in counts was ≤ 6. Methods for determing growth rates are presented in the results.

Statistical Analysis

Fish that had damaged fins or missing scales were eliminated only from the analysis of that character; consequently, comparisons between samples involved different sample sizes for different characters.

Bartlett's test for homogeneity of variances was used prior to all parametric tests. Following Conover (1971), nonparametric tests were used when variances were found to be heterogeneous ($p < 0.05$). Slopes from least squares regressions of metric measurements on standard length were compared by analysis of covariance (Steele and Torrie 1960). If slopes were not significantly different ($p > 0.05$), adjusted means were then compared by analysis of covariance. I used untransformed metric measurements in all regressions because coefficients of determination (R^2) varied little ($\pm$ 0.02) from regressions of log transformed data.

CHAPTER VIII

RESULTS

Morphological Variation

Meristic counts for yoy bluegills varied little among habitats. For each year, there were no significant differences in frequency distributions among habitats of either soft dorsal or anal fin rays (p's > 0.10). Similarly in 1981, there was no significant difference in the frequency distribution of dorsal spines among habitats ($p > 0.50$). In 1980, nearly all (94%) of the bluegills had 10 dorsal spines (Table 47). Apparently, the number of dorsal spines is either a conservative trait or selection occurs very early in the ontogeny of bluegills. Sample size relative to the range of counts of lateral line scales (LL) limited the number of habitats that could be meaningfully compared each year. In 1980, there was no significant difference in LL frequency distributions among fish from vegetated shallow, vegetated intermediate and nonvegetated shallow habitats ($p > 0.10$). However in 1981, the frequency distributions of lateral line scales were significantly different ($p < 0.05$) among fish from different depth categories in vegetated areas (Table 48). Inspection of frequency distributions and subsequent chi square tests indicated that the distributions of these scales for fish from shallow and intermediate depths were not significantly different ($T= 4.422$, 5 df, $p < 0.10$); but there was a significant difference in the distributions between fish collected at

Table 47. Frequency and relative frequency (% in parentheses) of dorsal spines for all samples of bluegills.

Year class	Year of collection	Age group	N	Dorsal spines 9	10	11	12
1979	1979	0+	50		48 (96.0)	2 (4.0)	
1980	1980	0+	164	3 (1.8)	154 (93.9)	7 (4.3)	
1981	1981	0+	430	6 (1.4)	367 (85.3)	54 (12.6)	3 (0.7)
1979	1980	I+	20		20 (100)		
1980	1981	I+	77	2 (2.6)	72 (93.5)	3 (3.9)	
$\leq$1977	1981	$\geq$IV+	10	1 (10.0)	8 (80.0)	1 (10.0)	

Table 48. Observed and, in parentheses, expected frequencies of lateral line scales for yoy bluegills collected in vegetated habitats in 1981. Expected frequencies were calculated assuming independence of depth. Shallow $\leq$ 50 cm; Intermediate = 51 - 150 cm; Deep > 150 cm.

	Lateral line scales						
Habitat	$\leq$ 40	41	42	43	44	45	$\geq$ 46
Shallow	11 (7.99)	12 (11.51)	15 (21.10)	23 (21.74)	18 (16.62)	12 (9.91)	3 (5.12)
Intermediate	12 (9.44)	16 (13.59)	27 (24.92)	30 (25.67)	14 (19.63)	8 (11.70)	4 (6.04)
Deep	2 (7.57)	8 (10.90)	24 (19.98)	15 (20.59)	20 (15.74)	11 (9.38)	9 (4.84)

$T = 22.109$ (12 df) $p < 0.05$

depths > 150 cm and those collected from shallower areas (T = 17.480, 6 df, $p < .01$). The difference between distributions is primarily in the tails. The distribution of LL scales for bluegills collected at depths > 150 cm is skewed to the right, while the distribution of LL scales for bluegills collected at depths $\leq$ 150 cm is skewed to the left (Figure 9). Since the differences in distributions is in the direction of skewness, comparisons with other habitats (which would have necessitated combining counts in either or both tails of the distribution) were not made.

In contrast to meristic counts, body form was quite variable between habitats. All least squares regressions of morphometric measurements on standard length (SL) of fish from each habitat were highly significant (all p's $\leq$ 0.0001). With the exception of regressions of head length (HL) on SL for 1980, variances were not significantly different among habitats (p's > 0.10). Since the variances associated with the regressions of HL on SL for 1980 was barely within the rejection region (Bartlett's test, T = 9.588, 4 df, $X^2_{(.05)} = 9.488$), I elected to ignore this difference in variances. Analysis of covariance indicated that the slopes for the regression of HL on SL were significantly different (p's = 0.001) among fish from each habitat each year (Tables 49 and 50). Each year, HL (as a function of SL) showed a greater increase per incremental increase in length for bluegills collected at depths $\leq$ 50 cm compared to those collected at greater depths (Table 51). Note that the weakest relationship between HL and SL occurred in vegetated areas at intermediate depths (51 to 150 cm) each year. This increased variability at intermediate depths could result from the mixing of phenotypes associated with greater and lesser

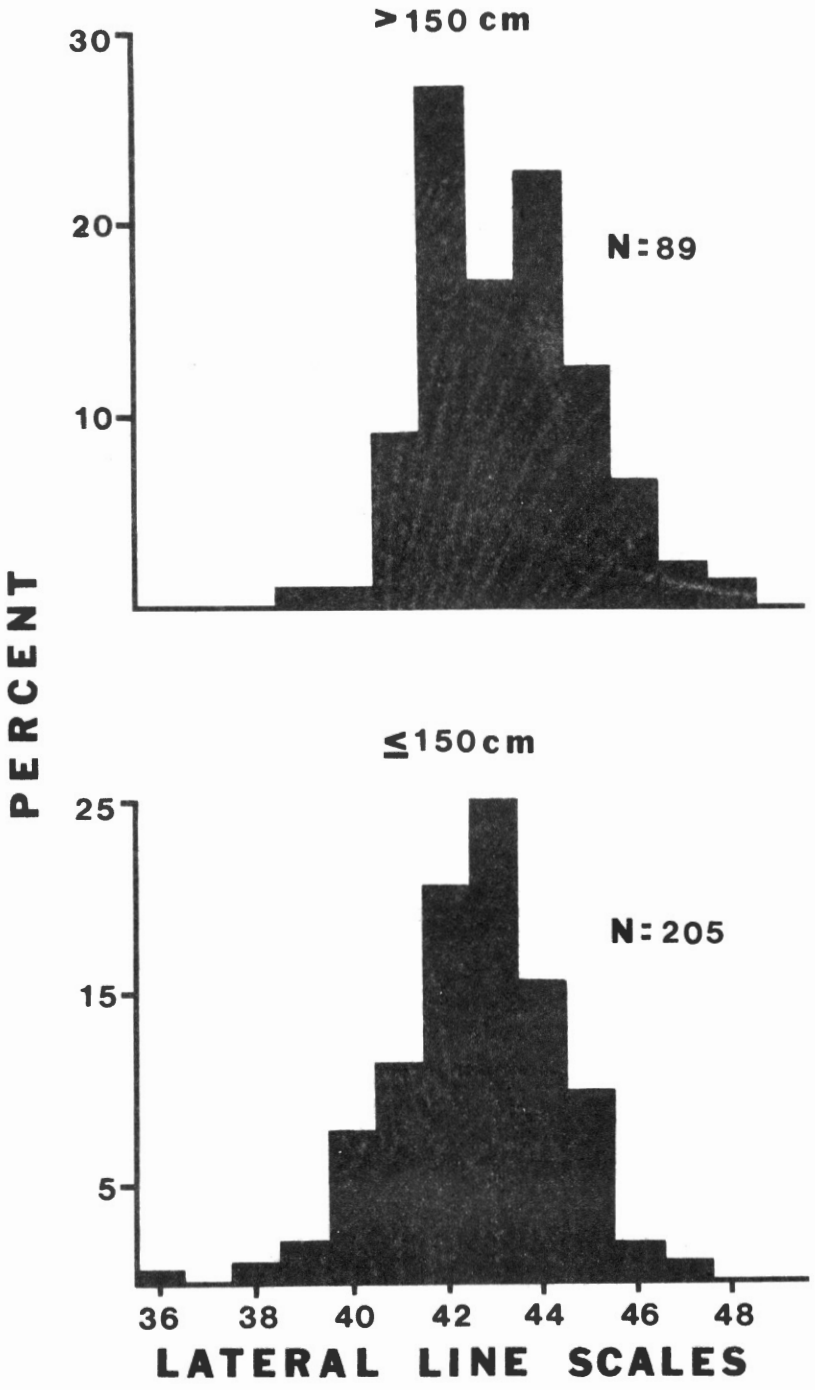

Figure 9. Frequency distributions of lateral line scale counts of yoy bluegills collected at different depths.

Table 49. Analysis of covariance for homogeneity of slopes among habitats for least squares regressions of head length (HL) on standard length (SL) for yoy bluegills collected in 1980. All regression coefficients compared are highly significant (p = 0.0001).

Source	df	Sum of squares	Mean square	F	p
Among	9	449.1176	49.9020	227.91	0.0001
Error	229	50.1404	0.2190		
Corrected total	238	499.2580			

Source	df	Sum of squares	Mean square	F	p
Habitat	4	3.7787	0.9447	4.31	0.0022
SL	1	195.1550	195.1550	891.31	0.0001
Habitat*SL	4	4.4701	1.1175	5.10	0.0006

Table 50. Analysis of covariance for homogeneity of slopes among habitats for least squares regressions of head length (HL) on standard length (SL) for yoy bluegills collected in 1981. All regression coefficients compared are highly significant (p = 0.0001).

Source	df	Sum of squares	Mean square	F	p
Among	9	157.5688	17.5076	102.99	0.0001
Error	173	29.4102	0.1700		
Corrected total	182	186.9790			

Source	df	Sum of squares	Mean square	F	p
Habitat	4	2.6986	0.6747	3.97	0.0042
SL	1	106.8723	106.8723	628.66	0.0001
Habitat*SL	4	3.3068	0.8267	4.86	0.0010

Table 51. Least squares regressions of head length (HL) on standard length (SL) of yoy bluegills for each habitat, where HL = $b_0 + b_1(SL)$. All regression coefficients are highly significant ($p = 0.0001$). Vegetation: P = present, A = absent; Depth: S = shallow ($\leq$ 50 cm), I = intermediate (51-150 cm), D = deep (> 150 cm).

	1980			1981		
Habitat	b_0	b_1	R^2	b_0	b_1	R^2
PS	-1.747	0.415	.92	-0.216	0.357	.82
PI	0.618	0.327	.69	2.085	0.262	.69
PD	0.688	0.328	.94	1.558	0.278	.86
AS	-0.503	0.365	.91	-1.664	0.412	.94
AI	0.815	0.308	.90			
AD				0.478	0.310	.75

depths, as well as any phenotype associated with intermediate depths.

Analysis of covariance indicated that the slopes for regressions of caudal peduncle depth (CP) on SL were not significantly different among habitats for either year (p 's > 0.40). However, each year there was a significant difference among habitats in mean CP adjusted for SL (Tables 52 and 53). In both years, fish collected from shallow habitats had a greater adjusted mean CP, though all comparisons between means were not significant.

Slopes for regressions of body depth (BD) on SL were not significantly different among habitats each year (both p's > 0.50). However, mean BD adjusted for SL was significantly different ($p \leq 0.0002$) among habitats each year (Tables 54 and 55). In both years, fish collected from shallow vegetated areas had a significantly greater body depth. Comparisons of adjusted mean BD between fish from most other habitats were not significantly different. Nevertheless, it is interesting that the ordering of adjusted means remained the same for those habitats which appeared both years in the analysis.

The three metric measurements indicate the same basic trend among habitats for both years. Bluegills collected from shallow areas, especially when vegetation was present, have a more gibbose body form with a larger head. Fish collected from deeper areas had smaller heads and were more fusiform in shape. Additionally, the significant difference in lateral line scale counts indicates differences in phenotypes related to depth.

Weight-length relationships were also significantly different among fish from different habitats (Tables 56 and 57). Each year fish collected from depths $\leq$ 50 cm showed a greater increase in weight per

Table 52. Analysis of covariance for mean caudal peduncle depth (CP) adjusted for standard length (SL) of yoy bluegills among habitats for 1980. Regression coefficients for least squares regressions of CP on SL were not significantly different among habitats ($F = 0.63$, $p > 0.60$). A common slope of 0.1433 ± 0.0036 ($p = 0.0001$) was used in the calculation of adjusted means (least squares means, LSM).

Source	df	Sum of squares	Mean square	F	p
Among	5	64.9254	12.9851	338.09	0.0001
Error	233	8.9489	0.0384		
Corrected total	238	73.8743			

Source	df	Sum of squares	Mean square	F	p
Habitat	4	0.4189	0.1047	2.73	0.0301
SL	1	60.9716	60.9716	1587.51	0.0001

Habitat*	Least squares means ± S.E.
PS	3.600 ± 0.019
AS	3.539 ± 0.027
AI	3.521 ± 0.045
PD	3.516 ± 0.051
PI	3.499 ± 0.030

	$p > \|T\|$ H_o: LSM(i) = LSM(j)			
i/j	AS	AI	PD	PI
PS	0.063	0.104	0.119	0.005
AS		0.736	0.692	0.331
AI			0.941	0.684
PD				0.774

*P = vegetation present, A = vegetation absent; Depth categories: S = shallow (≤ 50 cm), I = intermediate (51 - 150 cm), D = deep (> 150 cm).

Table 53. Analysis of covariance for mean caudal peduncle depth (CP) adjusted for standard length (SL) of yoy bluegills among habitats for 1981. Regression coefficients for least squares regressions of CP on SL were not significantly different among habitats ($F = 0.98$, $p > 0.40$). A common slope of 0.1211 ± 0.0050 ($p = 0.0001$) was used in the calculation of adjusted means (least squares means, LSM).

Source	df	Sum of squares	Mean square	F	p
Among	5	23.0350	4.6070	128.07	0.0001
Error	177	6.3672	0.0360		
Corrected total	182	29.4022			

Source	df	Sum of squares	Mean square	F	p
Habitat	4	0.8542	0.0214	5.94	0.0002
SL	1	20.9889	20.9889	583.46	0.0001

Habitat*	Least squares means ± S.E.	i/j	p > |T| H_o: LSM(i) = LSM(j) AS	PI	PD	AD
PS	3.456 ± 0.026	PS	0.385	0.132	<0.001	<0.001
AS	3.399 ± 0.060	AS		0.989	0.263	0.032
PI	3.398 ± 0.028	PI			0.060	0.003
PD	3.326 ± 0.026	PD				0.092
AD	3.238 ± 0.045					

*P = vegetation present, A = vegetation absent; Depth categories: S = shallow (≤ 50 cm), I = intermediate (51 - 150 cm), D = deep (> 150 cm).

Table 54. Analysis of covariance for mean body depth (BD) adjusted for standard length (SL) of yoy bluegills among habitats for 1980. Regression coefficients for least squares regressions of BD on SL were not significantly different among habitats ($F = 0.73$, $p > 0.50$). A common slope of 0.4156 ± 0.0094 ($p = 0.0001$) was used in the calculation of adjusted means (least squares means ,LSM).

Source	df	Sum of squares	Mean square	F	p
Among	5	549.3031	109.8606	415.46	0.0001
Error	233	61.6123	0.2644		
Corrected total	238	610.9154			

Source	df	Sum of squares	Mean square	F	p
Habitat	4	6.4561	1.6140	6.10	0.0001
SL	1	513.2186	513.2186	1940.84	0.0001

Habitat*	Least squares means ± S.E.	i/j	p > |T| H_o: LSM(i) = LSM(j) AS	AI	PI	PD
PS	9.878 ± 0.049	PS	0.014	0.023	<0.001	0.001
AS	9.664 ± 0.072	AS		0.566	0.178	0.086
AI	9.584 ± 0.118	AI			0.648	0.310
PI	9.519 ± 0.079	PI				0.455
PD	9.403 ± 0.113					

*P = vegetation present, A = vegetation absent; Depth categories: S = shallow (≤ 50 cm), I = intermediate (51 - 150 cm), D = deep (> 150 cm).

Table 55. Analysis of covariance for mean body depth (BD) adjusted for standard length (SL) of yoy bluegills among habitats for 1981. Regression coefficients for least squares regressions of BD on SL were not significantly different among habitats ($F = 0.67$, $p > 0.60$). A common slope of 0.3998 ± 0.0114 ($p = 0.0001$) was used in the calculation of adjusted means (least squares means, LSM).

Source	df	Sum of squares	Mean square	F	p
Among	5	247.5932	49.5186	265.26	0.0001
Error	177	33.0423	0.1867		
Corrected total	182	280.6355			

Source	df	Sum of squares	Mean square	F	p
Habitat	4	4.4317	1.1080	5.93	0.0002
SL	1	228.5857	228.5857	1224.48	0.0001

Habitat*	Least squares means ± S.E.
PS	9.611 ± 0.059
AS	9.406 ± 0.137
PI	9.394 ± 0.063
PD	9.330 ± 0.059
AD	9.083 ± 0.102

	$p > \|T\|$ H_o: LSM(i) = LSM(j)			
i/j	AS	PI	PD	AD
PS	0.169	0.013	<0.001	<0.001
AS		0.937	0.613	0.061
PI			0.469	0.010
PD				0.039

*P = vegetation present, A = vegetation absent; Depth categories: S = shallow ($\leq$ 50 cm), I = intermediate (51 - 150 cm), D = deep (> 150 cm).

Table 56. Analysis of covariance for homogeneity of slopes among habitats for least squares regressions of log weight (WT) on log total length (TL) for yoy bluegills collected in 1980. All regression coefficients compared are highly significant (p = 0.0001).

Source	df	Sum of squares	Mean square	F	p
Among	9	7.82295	0.86922	742.56	0.0001
Error	229	0.26806	0.00117		
Corrected total	238	8.09101			

Source	df	Sum of squares	Mean square	F	p
Habitat	4	0.05941	0.01485	12.69	0.0001
TL	1	4.05846	4.05846	3467.11	0.0001
Habitat*TL	4	0.05759	0.01440	12.30	0.0001

Table 57. Analysis of covariance for homogeneity of slopes among habitats for least squares regressions of log weight (WT) on log total length (TL) for yoy bluegills collected in 1981. All regression coefficients compared are highly significant (p = 0.0001).

Source	df	Sum of squares	Mean square	F	p
Among	9	4.12723	0.45858	411.15	0.0001
Error	173	0.19296	0.00112		
Corrected total	182	4.32019			

Source	df	Sum of squares	Mean square	F	p
Habitat	4	0.01296	0.00324	2.90	0.0233
TL	1	3.02186	3.02186	2709.30	0.0001
Habitat*TL	4	0.01363	0.00341	3.05	0.0183

incremental increase in length than did fish collected at greater depths (Table 58).

Bluegill Spawning Dates

Daily rings begin forming on bluegill otoliths on the first day of swim-up (Taulbert and Coble 1977). In most fish the time from egg fertilization to hatching is negatively correlated with water temperature. However, there is no such consistent relationship between fertilization and hatching time over a temperature range of 21-27 ^{o}C for bluegills [see Carlander (1977) for a general review]. For calculating spawning dates and daily growth rates, I assumed that bluegills in Rush Lake were 5.0 mm long at time of swim-up, and that this stage occurred 6 days after egg fertilization (Toetz 1966; Meyer 1970). Analysis of variance indicated that there were no significant differences in either mean collection date or mean date of swim-up of bluegills among habitats ($p's > 0.10$). Therefore, estimated dates of fertilization were combined to determine the frequency distribution of bluegill spawning activity (Figure 10).

All fish used for growth analysis originated from eggs spawned between April 12 and July 4. The estimated date of the earliest spawned eggs agrees well with my observations of bluegill nesting activity. Shortly after the drop in water temperature and herbicide application, bluegills apparently resumed spawning. Three major peaks in bluegill spawning occurred at approximately 2 week intervals between April 24 and May 25. There are several independent indications that the estimated distribution of bluegill spawning activity is biased towards spawning which occurred before June 1. Firstly, my observations that bluegill

Table 58. Least squares regressions of log weight (WT) on log total length (TL) for each habitat, where log WT = log b_0 + $b_1$log(TL). All slopes and intercepts are highly significant ($p = 0.0001$). Vegetation: P = present, A = absent; Depth: S = shallow ($\leq$ 50 cm), I = intermediate (51-150 cm), D = deep (> 150 cm).

	1980			1981		
Habitat	b_0	b_1	R^2	b_0	b_1	R^2
PS	-5.092	3.162	.98	-5.186	3.226	.94
PI	-4.718	2.919	.90	-4.634	2.851	.92
PD	-4.838	3.000	.98	-4.645	2.855	.96
AS	-5.199	3.226	.99	-5.239	3.249	.98
AI	-3.896	2.393	.89			
AD				-4.846	2.995	.98

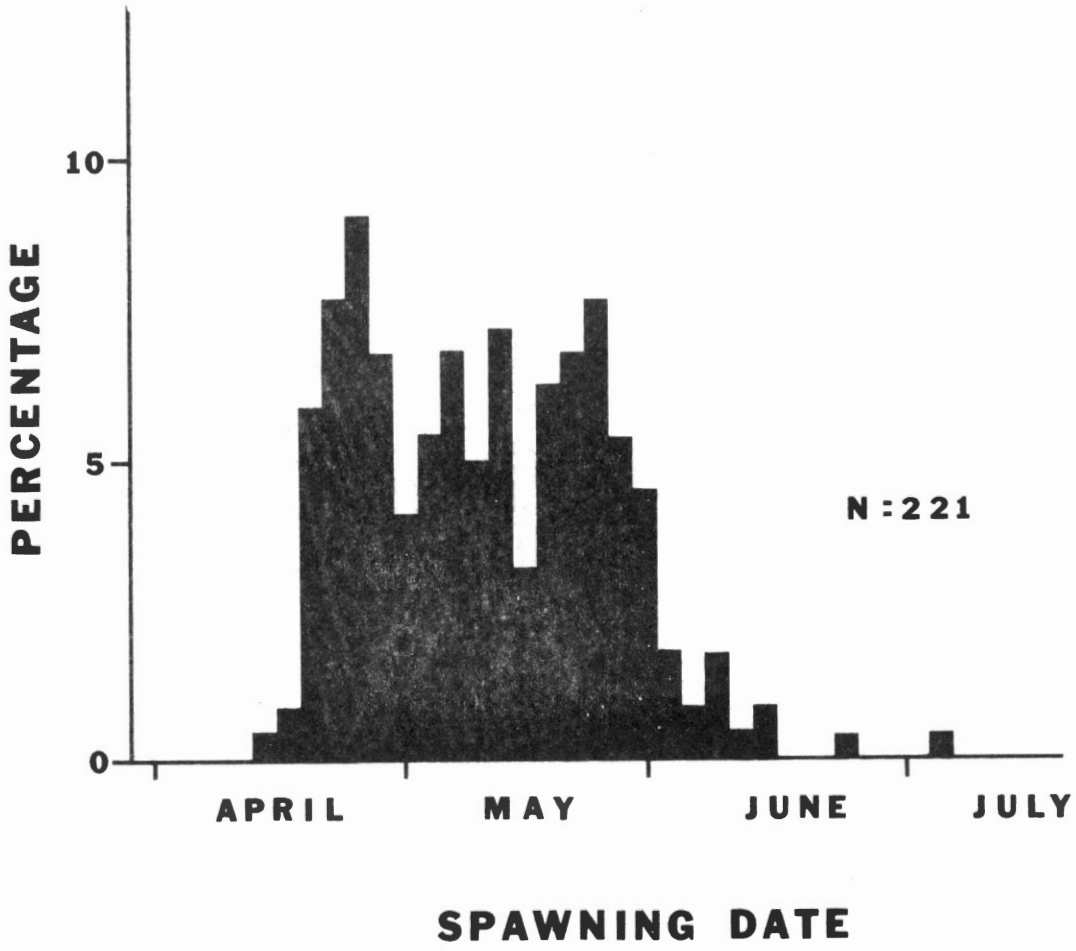

Figure 10. Estimated spawning season of bluegills based on analysis of otoliths from yoy bluegills collected in 1981.

nesting activity continued at least until early August is not reflected in the estimated spawning season. Secondly, the earliest spawned bluegills would be subjected to the greatest cummulative trapping effort, thereby increasing their probability of eventual capture. Thirdly, the previously demonstrated size selectivity of minnow traps would decrease the probability of capturing the smaller and presumably later-spawned fish. However, there were no significant differences between mean lengths of bluegills used for age analysis and all yoy bluegills collected each sampling period (Table 59). Therefore, the distribution of spawning dates most likely reflects the dates of fertilization for most bluegills collected.

Mortality of YOY Bluegills

Estimates of mean date of fertilization were significantly different among sampling dates (Kruskall-Wallis test, $T = 143.522$, 4 df, $p < 0.001$; the first two samples were not included in this analysis because of small sample size). Not only were the means different among samples, but the range in fertilization dates also changed over time. Fish originating from the earliest spawning were not represented in September samples (Figure 11). The absence of early spawned fish from September samples is not a function of sampling error, since the mean length of bluegills used for age analysis was not significantly different from the mean length of all yoy bluegills collected, and large numbers of I+ fish were always collected (Figure 12). Therefore, changes in estimated dates of fertilization between samples most likely resulted from the cumulative effects of mortality of older fish. It is unknown whether or not this mortality was continuous; however, it

Table 59. Comparison of mean total lengths of bluegills that were aged and all yoy bluegills collected for each sampling period.

Sampling period	Total length (mm)								
	All			Aged					
	$\bar{X}$	S.E.	N	$\bar{X}$	S.E.	N	t	df	p
17 June	19.0	0.71	5	19.7	0.88	3	0.486	6	>0.50
1 July	24.4	0.86	10	24.0	1.35	4	0.248	12	>0.50
14 July	29.5	0.31	61	29.3	0.53	25	0.339	84	>0.50
3 August	30.9	0.22	218	31.0	0.53	45	0.189	261	>0.50
11 August	31.5	0.27	189	32.6	0.50	41	1.746	228	>0.05
2 September	32.3	0.22	264	32.9	0.50	57	1.154	319	>0.30
22 September	33.7	0.24	327	33.8	0.75	46	0.145	371	>0.50

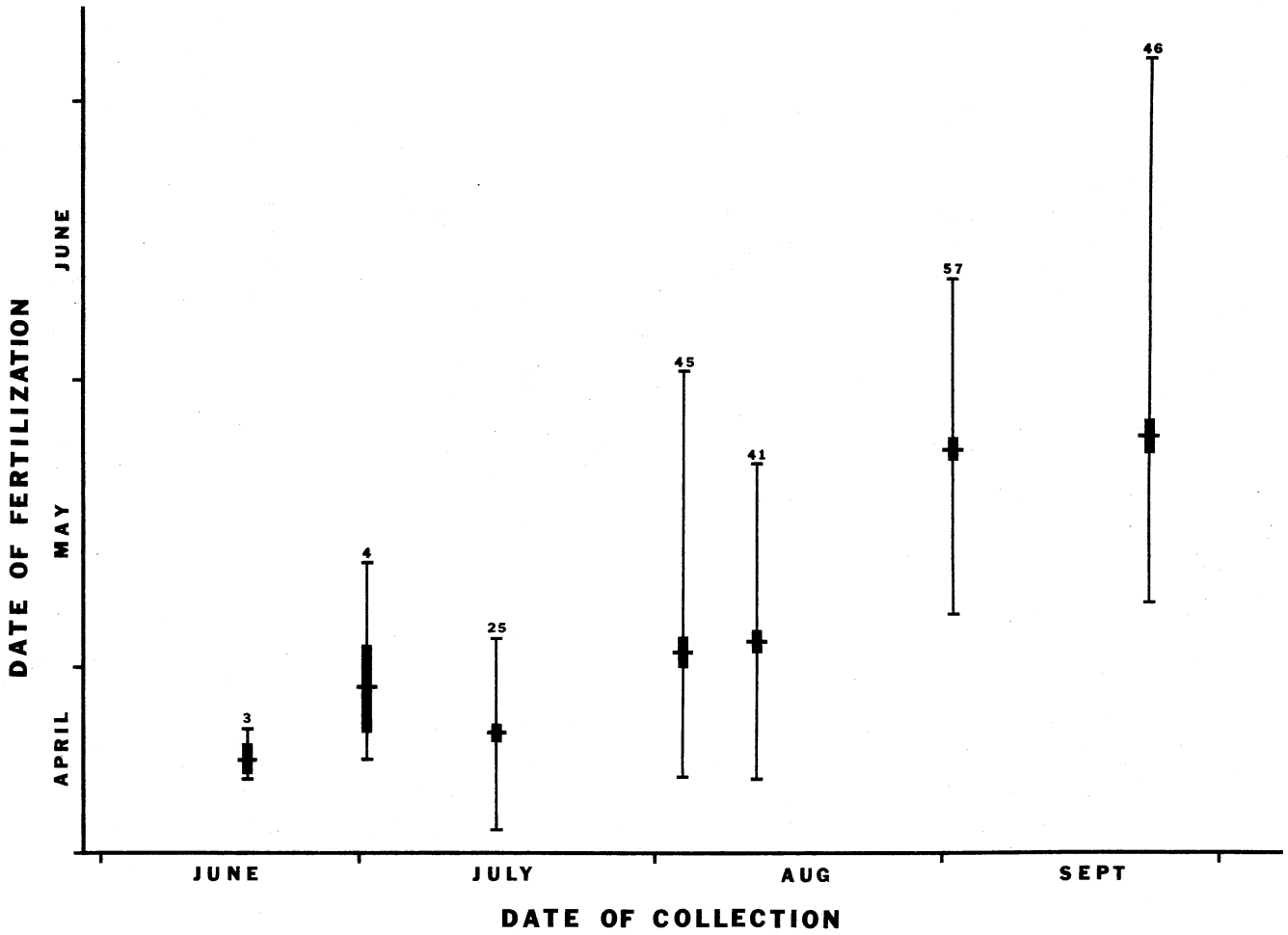

Figure 11. Means, standard errors, and ranges for estimated dates of fertilization for yoy bluegills collected in 1981. Sample sizes are given above the upper range limit.

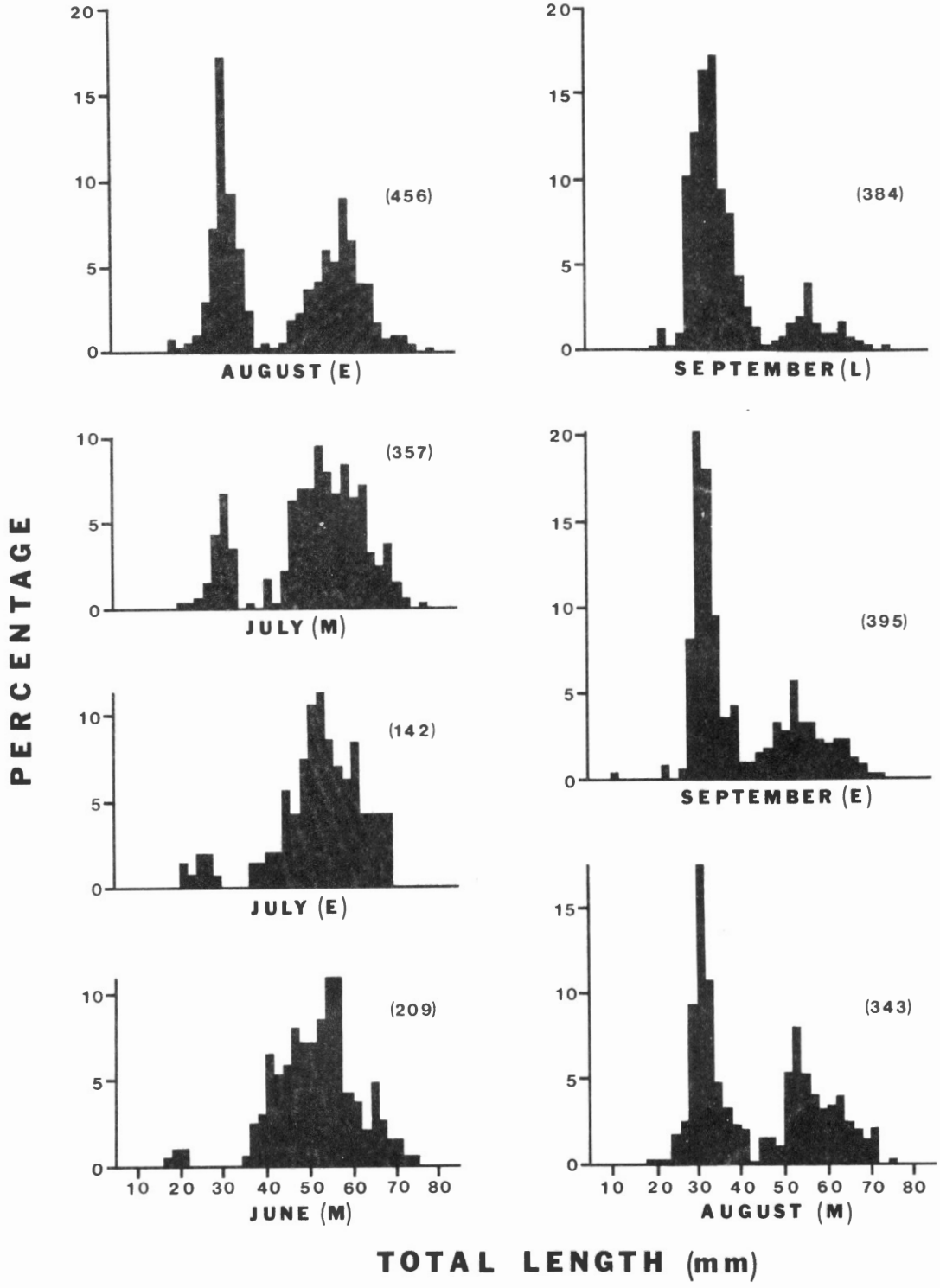

Figure 12. Length frequency distributions for each sample of bluegills collected by minnow traps in 1981. Bimodal distributions represent ages 0+ and I+.

appears that substantial mortality occurred between the middle of July and early September.

Habitat Specific Growth Rates

Daily growth rate (GR) of aged bluegills was calculated by:

$$GR = (TL - 5 \text{ mm}) / Age \quad (1)$$

where (TL - 5 mm) = total length at capture corrected for length at swim-up, and age = age in days from day of swim-up. Regressions of GR on age were highly significant for bluegills collected from vegetated habitats ($p = 0.0001$), but there was no significant relationship between these variables for fish collected from nonvegetated habitats; however, sample sizes from nonvegetated habitats were small. GR's for fish from nonvegetated shallow and intermediate habitats were 0.305 and 0.289 mm/day, respectively. Analysis of covariance indicated that there was no significant difference ($p > 0.05$) among fish from vegetated habitats in slopes for regressions of GR on age, but mean GR's adjusted for age were significantly different among fish from the three habitats (Table 60). Bluegills collected from depths $\leq$ 50 cm had the greatest adjusted GR, while bluegills collected from intermediate depths had the lowest GR.

Seasonal Growth Rates

Since the frequency distribution among habitats of bluegills used for age analysis was similar to the distribution of all bluegills collected in 1981, I combined all bluegills aged within each sampling period to estimate the mean seasonal GR (Equation 1) for the bluegill population as a whole (Table 61). There was a highly significant

Table 60. Analysis of covariance for growth rate (GR, mm/day) adjusted for age of yoy bluegills among vegetated habitats for 1981. Regression coefficients for least squares regressions of GR on age were not significantly different among habitats (F = 0.95, p = 0.39). A common slope of -0.0016 ± 0.0002 (p = 0.0001) was used in the calculation of adjusted means (least squares means, LSM).

Source	df	Sum of squares	Mean square	F	p
Among	3	0.125013	0.041671	37.15	0.0001
Error	191	0.214255	0.001122		
Corrected total	194	0.339268			

Source	df	Sum of squares	Mean square	F	p
Habitat	2	0.020319	0.010160	9.06	0.0002
Age	1	0.100963	0.100963	90.00	0.0001

Habitat*	Least squares means $\pm$ S.E.
PS	0.305 ± 0.005
PI	0.280 ± 0.004
PD	0.290 ± 0.005

	$p > \|T\|$ H_o: LSM(i) = LSM(j)	
i/j	PI	PD
PS	0.0001	0.0230
PI		0.0899

*Depth categories: S = shallow ($\leq$ 50 cm), I = intermediate (51 - 150 cm), D = deep (> 150 cm); P = vegetation present

Table 61. Comparison of estimated daily growth rates of yoy bluegills calculated by different methods.

Collection date	N	Mean age[1] of bluegills (days)	Mean growth rate (mm/day)		
			Overall[2] ± S.E.	Between[3] samples	Between[4] samples
17 June	3	51.5	0.286 ± 0.023		
30 June	4	56.9	0.335 ± 0.005	0.796	0.415
14 July	25	76.1	0.319 ± 0.007	0.276	0.371
3 August	45	87.8	0.297 ± 0.005	0.145	0.065
11 August	41	94.3	0.294 ± 0.006	0.246	0.075
2 September	57	94.5	0.296 ± 0.005	0.284[5]	0.038
23 September	46	114.0	0.254 ± 0.006	0.046	0.067

[1] Age from day of swim up.

[2] Calculated from day of swim-up to collection date [(TL - 5 mm) / Age].

[3] Growth rate = $(\overline{TL_i} - \overline{TL_h}) / (\overline{Age_i} - \overline{Age_h})$; where h and i are consecutive samples. See Table 60 for total lengths of aged bluegills.

[4] Growth rate = $(\overline{TL_i} - \overline{TL_h}) / (\text{Collection date}_i - \text{Collection date}_h)$. Total length is for all bluegills collected, see Table 60 for sample sizes and lengths.

[5] Calculated from collection date 215 to 244 because there was no significant difference between mean ages for collection dates 11 August and 2 September ($t = 0.102$, 96 df, $p > 0.90$).

positive correlation between GR and total length (Table 62). This is not surprising since we should expect faster-growing individuals to be of a larger size than similar ages of slower-growing fish. There were highly significant, negative correlations between GR and age, and between GR and date of collection. Because age and date of collection were also highly correlated, it is unknown which, if either, variable influenced GR. However the weak, though significant, association between GR and and date of fertilization indicates that there was little difference in GR between early and late-spawned fish. Since date of fertilization and date of collection were strongly associated but there was little correlation between GR and date of fertilization, I suggest that GR is influenced at least partially by age, or that age is significantly associated with one or more unmeasured variables such as physiological changes that control GR.

There was no significant difference among collection dates in slopes of regressions of GR on age ($F_{(4,204)} = 2.11$, $p = 0.0806$). Similarly, GR's adjusted for age were not significantly different ($F_{(4, 208)} = 1.76$, $p > 0.10$). However, unadjusted means differed significantly (Table 63). Significant differences among unadjusted means but not among adjusted means indicates that the difference is the result of the covariate (in this case age) and not treatment differences (Steele and Torrie 1960).

I used the following equation as an additional method of calculating seasonal GR:

$$GR = (\overline{TL_i} - \overline{TL_h}) \; / \; (\overline{Age_i} - \overline{Age_h}) \qquad (2)$$

where i and h are consecutive samples.

While the mean of the individual GR's [equation (1)] provides an

Table 62. Correlation matrix (Pearson product-moment) for variables that were significantly correlated with daily growth rates (mm/day) of aged bluegills (N = 221; probabilities in parentheses).

	Total length	Age (days)	Growth rate	Julian date of fertilization
Julian collection date	0.4421 (0.0001)	0.7800 (0.0001)	-0.4121 (0.0001)	0.7617 (0.0001)
Total length		0.6020 (0.0001)	0.3870 (0.0001)	0.0713 (0.2916)
Age			-0.4899 (0.0001)	0.1889 (0.0048)
Growth rate				-0.1391 (0.0388)

Table 63. Analysis of variance for differences among collection dates in mean growth rates (mm/day) for yoy bluegills.

Source	df	Sum of squares	Mean square	F	p
Among	4	0.08675	0.02169	15.61	.0001
Error	209	0.29035	0.00139		
Corrected total	213	0.37710			

estimate of the overall GR from day of swim-up to day of capture, equation (2) estimates the mean rate of growth between samples. If bluegills continued to grow at a constant rate throughout the summer then these two estimates would be equal. Both estimates provide similar estimates of GR for the period 14 July to 2 September (Table 61), except that GR decreased markedly between 14 July and 3 August, and then returned to the previous level by the next sampling period. A virtual cessation of growth between 2 and 22 September is reflected in both estimates: the between sample GR approached zero, while the overall GR declined as a result of little change in length over the 20 day period.

Additionally, I calculated mean GR for all bluegills collected each sampling period by simply dividing the difference in total length between samples by the mean number of days that elapsed between consecutive samples (Table 61). This method is commonly used to measure seasonal growth of fishes. Clearly, this method grossly underestimates GR, and further suggests that there was continuous recruitment of later-spawned fish and continuous mortality of older fish.

Natural Selection

Meristic characters of fish are determined genetically and by environmental factors during early development (see Barlow 1961 for a general review). Therefore, the strongest evidence for natural selection operating on meristic characters is obtained by following a cohort over time. Less convincing evidence for the occurrence of natural selection can be obtained by comparing cohorts of the same age, and if no statistically significant differences are found, subsequently comparing different age-year classes. Statistical comparisons of

meristic counts for both within and between cohorts are summarized in Tables 64, 65, and 66.

I followed each of two cohorts (the 1979 and 1980 year classes) over a two year period and made within cohort comparisons of meristic counts. I found only one instance of directional selection within a cohort. Samples of the 1979 year class collected in 1979 and 1980 had significantly different ($p < 0.025$) soft anal fin ray (AR) distributions (Table 67). A series of intercohort comparisons of yoy fish indicated that the AR distribution of the 1980 year class differed significantly from the other two year classes (Tables 68 and 69). However, there was no significant difference in the AR distribution between I+ fish of the 1979 and 1980 year classes, which indicates that after one season of selection on yoy bluegills, the AR distributions were similar among cohorts. If we assume that selection was similar among years, it appears that it was greatest during the first year of life of bluegills because there was no significant difference ($p > 0.10$) between the AR distributions of adults and I+ fish. (See Table 70 for AR frequency distributions for all cohorts.) Also, adult bluegills had significantly fewer AR's than yoy collected in 1981 (Table 71).

The frequency distributions of soft dorsal fin rays (DR) was remarkably similar between most samples (Table 72). The only significant difference in DR distributions was between yoy and adult bluegills collected in 1981 (Table 73); yoy fish had 12 or more DR more often then expected.

In most samples nearly all fish had 10 dorsal spines (Table 47). Consequently, I made only one statistical test and found that among yoy fish, the 1981 YC had 11 dorsal spines more frequently than expected

Table 64. Summary of chi square tests for independence of numbers of soft anal fin rays from habitat, collection method, year class, and age group. Samples from all collection methods for 1980 were combined for all between year comparisons. See text for habitat categories. Because of expected values of less than five, nonvegetated deep and intermediate habitats were combined for 1980, and nonvegetated shallow and intermediate habitats were combined for 1981. (Shock = Electrofishing).

Year classes	Age groups	Years of collections	Test for Independence of	Collection method	T	df	p
1980	0+	1980	Habitat	Traps	2.105	4	>.500
1980	0+	1980	Method of collection	Traps Seine Shock	2.629	2	>.100
1981	0+	1981	Habitat	Traps	5.685	4	>.100
1979 1980 1981	0+	1979 1980 1981	Year class	Traps Seine Shock	17.731	2	<.001
1979 1981	0+	1979 1981	Year class	Seine Traps	2.136	1	>.100
(1979+ 1981) 1980	0+	1979 1980 1981	Year class	Traps Seines Shock	15.996	1	<.001
1979	0+ I+	1979 1980	Age	Seine Shock	5.957	1	<.025
1980	0+ I+	1980 1981	Age	Traps Shock	1.287	1	>.100
1979 1980	I+	1980 1981	Year class	Shock	0.008	1	>.900

Table 64. (Continued).

Year classes	Age groups	Years of collections	Test for Independence of	Collection method	T	df	p
1981 ≤1977	0+ ≥IV+	1981	Age + Year class	Traps Angling	17.701	1	<.001
(1979+ 1980) ≤1977	I+ ≥IV+	1980 1981	Age + Year class	Shock Angling	1.030	1	>.100

Table 65. Summary of chi square tests for independence of numbers of soft dorsal fin rays from habitat, collection method, year class, and age group. Samples from all collection methods for 1980 were combined for all between year comparisons. See text for habitat categories. Because of expected values of less than five, nonvegetated deep and intermediate habitats were combined for 1980, and nonvegetated shallow and intermediate habitats were combined for 1981. (Shock = Electrofishing).

Year classes	Age groups	Years of collections	Test for independence of	Collection method	T	df	p
1980	0+	1980	Habitat	Traps	6.049	4	>.100
1980	0+	1980	Method of collection	Traps Seine Shock	1.831	2	>.100
1981	0+	1981	Habitat	Traps	4.208	4	>.100
1979 1980 1981	0+	1979 1980 1981	Year class	Traps Seine Shock	5.692	2	>.050
1979	0+ I+	1979 1980	Age	Seine Shock	0.002	1	>.900
1980	0+ I+	1980 1981	Age	Traps Shock	0.020	1	>.500
1979 1980	I+	1980 1981	Year class	Shock	0.029	1	>.500
1981 ≤1977	0+ ≥IV+	1981	Age + year class	Traps Angling	4.221	1	<.050
(1979+ 1980) ≤1977	0+ ≥IV+	1980 1981	Age+ Year class	Shock Angling	0.987	1	>.250

Table 66. Summary of chi square tests for independence of lateral line scale counts from habitat, year class, and age group. Samples from all collection methods for 1980 were combined for all between year comparisons. See text for habitat categories. Because of expected values of less than five, nonvegetated deep and intermediate habitats were combined for 1980, and nonvegetated shallow and intermediate habitats were combined for 1981. (Shock = Electrofishing).

Year classes	Age groups	Years of collections	Test for independence of	Collection method	T	df	p
1981	0+	1981	Habitat	Traps	22.109	12	<.050
1981	0+	1981	Habitat	Traps	17.480	6	<.010
1980 1981	0+	1980 1981	Year class	Traps Seine Shock	6.207	7	>.250
1979	0+ I+	1979 1980	Age	Seine Shock	2.144	2	>.100
1979 1980	I+	1980 1981	Year class	Shock	0.646	2	>.100
1981 ≤1977	0+ ≥IV+	1981	Age + year class	Traps Angling	15.330	5	<.010
(1979+ 1980) ≤1977	I+ ≥IV+	1980 1981	Age+ Year class	Shock Angling	7.878	5	>.100

Table 67. Observed and, in parentheses, expected frequencies of soft anal fin rays for yoy and one-year old bluegills of the 1979 year class. Expected frequencies were calculated assuming independence of age.

	Soft anal fin rays	
Age	≤ 10	≥ 11
0+	4 (7.86)	46 (42.14)
I+	7 (3.14)	13 (16.86)
T = 5.957	(1 df)	$p < 0.025$

Table 68. Observed and, in parentheses, expected frequencies of soft anal fin rays for yoy bluegills. Expected frequencies were calculated assuming independence of year class.

Year class	Soft anal fin rays	
	≤ 10	≥ 11
1979	4 (9.75)	46 (40.25)
1980	84 (62.02)	234 (255.98)
1981	69 (85.23)	368 (351.77)
$T = 17.731$	(2 df)	$p < 0.001$

Table 69. Observed and, in parentheses, expected frequencies of soft anal fin rays for yoy bluegills. Expected frequencies were calculated assuming independence of year class.

Year class	Soft anal fin rays	
	≤ 10	≥ 11
1979 + 1981	73 (94.98)	414 (392.02)
1980	84 (62.02)	234 (255.98)
$T = 15.996$	(1 df)	$p < 0.001$

Table 70. Frequency and relative frequency (% in parentheses) of soft anal fin rays for all samples of bluegills.

Year class	Year of collection	Age group	N	Soft anal fin rays					
				8	9	10	11	12	13
1979	1979	yoy	50			4 (8.0)	42 (84.0)	4 (8.0)	
1980	1980	yoy	318	1 (0.3)	2 (0.6)	81 (25.5)	218 (68.6)	16 (5.0)	
1981	1981	yoy	437	1 (0.2)	1 (0.2)	67 (15.3)	334 (76.4)	32 (7.3)	2 (0.5)
1979	1980	I+	20			7 (35.0)	12 (60.0)	1 (5.0)	
1980	1981	I+	76			25 (32.9)	49 (64.5)	2 (2.6)	
$\leq$1977	1981	$\geq$IV+	40		1 (2.5)	16 (40.0)	23 (57.5)		

Table 71. Observed and, in parentheses, expected frequencies of soft anal fin rays for 0+ and ≥IV+ bluegills collected in 1981. Expected frequencies were calculated assuming independence of age.

	Soft anal fin rays	
Age	≤ 10	≥ 11
0+	69 (78.79)	368 (358.21)
≥IV+	17 (7.21)	23 (32.79)
T = 17.70	(1 df)	p < 0.001

Table 72. Frequency and relative frequency (% in parentheses) of soft dorsal fin rays for all samples of bluegills.

Year class	Year of collection	Age group	N	Soft dorsal fin rays				
				9	10	11	12	13
1979	1979	yoy	50		1 (2.0)	33 (66.0)	16 (32.0)	
1980	1980	yoy	316		7 (2.2)	212 (67.1)	97 (30.7)	
1981	1981	yoy	434	1 (0.2)	19 (4.3)	245 (56.5)	160 (36.9)	9 (2.1)
1979	1980	I+	20			13 (65.0)	7 (35.0)	
1980	1981	I+	77		4 (5.2)	50 (64.9)	23 (29.9)	
≤1977	1981	≥IV+	40		1 (2.5)	30 (75.0)	8 (20.0)	1 (2.5)

Table 73. Observed and, in parentheses, expected frequencies of soft dorsal rays for yoy and adult bluegills collected in 1981. Expected frequencies were calculated assuming independence of age.

	Soft dorsal rays	
Age group	≤ 11	≥ 12
yoy	265 (271.02)	169 (162.98)
Adults	31 (24.98)	9 (15.02)

$T = 4.221$ (1 df) $p < 0.05$

(Table 74).

Because the range of lateral line (LL) scale counts is relatively large with respect to sample sizes of I+ and older fish (Table 75), and because the difference in LL distributions among fish collected from different habitats was primarily in the tails, much larger sample sizes than available would be needed to detect all but very large differences. Except for the previously noted differences in LL distributions among fish collected from different habitats, the only significant difference in distributions was between yoy and adult fish collected in 1981 (Table 76).

It is noteworthy that the adults and their offspring sampled in 1981 had significantly different distributions for three of the four meristic characters examined. It is unknown if these differences are due to environmental effects during early development, or are due to natural selection.

Table 74. Observed and, in parentheses, expected frequencies of dorsal spines for yoy bluegills. Expected frequencies were calculated assuming independence of year class.

	Dorsal spines	
Year class	≤ 10	≥ 11
1979+1980	205 (192.07)	9 (21.93)
1981	373 (385.93)	57 (44.07)

$T = 12.880$ (1 df) $p < 0.001$

Table 75. Frequency and relative frequency (% in parentheses) of lateral line scales for each sample of bluegills.

Lateral line scales	Age and year class					
	1979 0+	1980 0+	1981 0+	1979 I+	1980 I+	≤1977 ≥IV+
36			1 (0.3)			
37						
38			2 (0.6)			
39	2 (10.5)	7 (3.6)	5 (1.5)			
40	4 (21.1)	21 (10.9)	20 (6.0)	3 (15.0)	3 (6.3)	3 (7.5)
41	3 (15.8)	23 (12.0)	41 (12.3)	2 (10.0)	5 (10.4)	5 (12.5)
42	4 (21.1)	37 (19.3)	72 (21.6)	4 (20.0)	9 (18.8)	8 (20.0)
43	1 (5.3)	47 (24.5)	75 (22.5)	4 (20.0)	13 (27.1)	6 (15.0)
44	4 (21.1)	29 (15.1)	60 (18.0)	4 (20.0)	10 (20.8)	4 (10.0)
45	1 (5.3)	20 (10.4)	42 (12.6)	1 (5.0)	6 (12.5)	6 (15.0)
46		7 (3.6)	10 (3.0)	2 (10.0)	2 (4.2)	6 (15.0)
47		1 (0.5)	5 (1.5)			2 (5.0)
48			1 (0.3)			
N	19	192	334	20	48	40

Table 76. Observed and, in parentheses, expected frequencies of lateral line scales for 0+ and ≥ IV+ bluegills collected in 1981. Expected frequencies were calculated assuming independence of age and year class.

Age group	Lateral line scales					
	≤ 41	42	43	44	45	≥ 46
0+	69 (68.72)	72 (71.40)	75 (72.29)	60 (57.12)	42 (42.84)	16 (21.42)
≥IV+	8 (8.28)	8 (8.60)	6 (8.71)	4 (6.88)	6 (5.16)	8 (2.58)

$T = 15.330$ (5 df) $p < 0.01$

CHAPTER IX

DISCUSSION

Morphology of fish is highly variable both within and between populations. Although genotype defines the general range of morphological phenotypes, the environment (especially during early development) has a profound influence in determining the phenotype within this range. The influence of environment and genotype in determining the phenotype has been demonstrated many times, and perhaps most convincingly by Harrington and Crossman (1976) using three different homozygous clones of the cyprinodont Rivulus marmoratus. To facilitate discussion of phenotypic differences among bluegills collected from different habitats, all statistical tests showing significant differences are summarized in Table 77. To highlight any apparent trends within or between habitats, the variables tested were assigned ranks; although, this does not imply that all habitats were significantly different from each other. Because similar trends were noted for vegetated and nonvegetated habitats, and because frequently there were no significant differences between vegetated and nonvegetated areas of similar depth, the following discussion is largely confined to differences among depth categories.

Ranks for each phenotypic trait consistently indicate that bluegills collected from shallow ($\leq$ 50 cm) areas were more robust, and grew faster in both length and weight. Interpretation of body form of

Table 77. Ranking of habitats in order of decreasing values (greatest = 1) for phenotypic characteristics showing a significant difference between two or more habitats. Ranked data are from Tables 48, 51 through 55, 58 and 60.

Characteristic[1]	Year	Habitat[2] PS	PI	PD	AS	AI	AD
LL (unadjusted means)	1981	3	2	1			
HL on SL (slopes)	1980	1	4	3	2	5	
	1981	2	5	4	1		3
CP (adjusted for SL)	1980	1	5	4	2	3	
	1981	1	3	5	2		4
BD (adjusted for SL)	1980	1	4	5	2	3	
	1981	1	3	4	2		5
log WT on log TL (slopes)	1980	2	4	3	1	5	
	1981	2	5	4	1		3
GR (adjusted for TL)	1981	1	3	2			

[1]LL = lateral line scales; HL = head length; CP = caudal peduncle depth; BD = body depth; WT = weight; SL = standard length; TL = total length; GR = growth rate.

[2]P = vegetation present; A = vegetation absent; S = shallow ($\leq$ 50 cm); I = intermediate (51 - 150 cm); D = deep (> 150 cm).

bluegills from the remaining depth categories is more complex. While bluegills from the deepest areas sampled (> 150 cm) had the smallest body depth, which indicates a more fusiform body shape, they grew in weight and length at a rate similar to fish from intermediate depths (51-150 cm). If we assume that the density (weight per unit volume) of all bluegills was similar, then it seems likely that bluegills from deeper areas became thicker bodied faster (a trait not measured) than those from intermediate depths.

Martin (1949) demonstrated that the growth of a body part or dimension relative to body length (relative growth) proceeds through several stanzas during the life of a fish. Within each stanza, relative growth for log transformed data is linear, and transitions between stanzas are marked by abrupt changes in the slope. Martin hypothesized that differences in intercepts for parallel lines implies that body size at time of transition between stanzas controls future body proportions. Furthermore, the time of inflection in relative growth lines may vary between different body parts. Martin concluded that the period of early development exerted a greater influence on future body form than did the subsequent growth rate.

Since evidence of growth stanzas has been reported for a variety of species of fish including at least one centrarchid (see Martin [1949] for a review), it is likely that such stanzas occur in bluegills. However, graphical analysis of body dimensions plotted against standard length of bluegills did not reveal any change in slopes. Therefore, for those regressions which were parallel but differed in adjusted means (BD, CP), it appears likely that differences in body form were established at an earlier stage of development and were maintained until

the fish were collected. Shortly after swim-up, larval bluegills move to the limnetic zone where they remain until they reach a size of 21 to 25 mm TL, and then they move back to the littoral zone (Werner 1967). Since the samples of bluegills collected from each habitat included individuals of a size which would have just returned from the limnetic zone, body form in these fish must have been established either during the limnetic phase or during an earlier stage of development.

The significant differences among regression lines indicate that there were specific associations between phenotype and habitat. The consistency in these associations indicates that the observations were not due to chance, and that they must be of some adaptive significance. Larson (1976) found that morphologically distinct phenotypes of threespine sticklebacks (Gasterosteus aculeatus) lived in different habitats within a lake. Moreover, he determined experimentally that there were also behavioral differences between phenotypes; the limnetic form was more fusiform and a more efficient planktivore, while the benthic form was more robust, aggressive, and more efficient in foraging macrobenthic items. While bluegills from depths > 150 cm in Lake Rush were more fusiform than those from in shallower areas, there was no indication that they foraged more on zooplankton; instead, benthic ostracods appeared to be more important in the diet of fish from deeper areas (recall Tables 34 and 35).

Since body form of bluegills is apparently established prior to the time when they return to the littoral zone, we are confronted by a rather perplexing question: "What is the mechanism maintaining the observed associations between habitat and phenotype?". These observed associations could have resulted from a number of mechanisms. If we

assume that yoy bluegills did not actively select habitats after leaving the limnetic zone, then Levene's original model could explain the observed phenotypic differences between habitats. His model assumes random breeding followed by a random dispersal of offspring to all available habitats, after which slection favors different alleles in each habitat. Levins and MacArthur (1966) pointed out that Levene's model also assumes that mortality within the habitat is density independent.

The observed phenotypic differences among habitats could have resulted from active selection of habitat, in which case different phenotypes selected different habitats, and presumably those habitats where their relative fitness was greatest. We might expect that such an active habitat selection by different phenotypes would evolve as a mechanism which would increase an individual's fitness. Casterlin and Reynolds (1978) concluded that yoy bluegills collected from a lake actively selected habitats when presented with a choice in laboratory experiments. However, because prior experience in a habitat may influence future habitat selection (Sale 1971), it is difficult to establish the causal mechanism of habitat selection by wild fish in the laboratory. Furthermore, for some species of fish, it is not simply prior experience which determines future habitat selection, but rather it is the ontogenetic stage at which this experience occurs. Quertermus (1975) found that Tilapia mossambica selected those habitats in which they were conditioned during their first 60 days of free swimming, but there was no selection of conditioning habitats when the conditioning occurred at a later stage of development.

Obviously yoy bluegills leaving the limnetic zone would have to

pass through two of the deeper depth categories (habitats that I arbitrarily defined) before they reached the shallowest habitat. From this pattern of movement we can infer that if prior experience influences future habitat selection, it most likely occurs only after yoy bluegills have spent some time in one or more littoral habitats. Furthermore, if habitat selection by bluegills is the result of prior experience, then the observed phenotypic differences between habitats must have resulted from differing selection pressures within each habitat during the course of evolution.

Habitat selection by fish is also influenced by intraspecific and interspecific interactions. Werner and Hall (1979) demonstrated competitively induced habitat shifts by sunfish. Similarly, Casterlin and Reynolds (1978) found that yoy bluegills avoided preferred habitats that were occupied by larger conspecifics. The presence of a predator also influences bluegill behavior and may affect habitat selection (Savino and Stein 1982). Consequently, the observed associations between phenotype and habitat may have resulted from intraspecific or interspecific interactions.

If interspecific interactions were an important determinant of bluegill habitat utilization, then the observed associations between phenotype and habitat would indicate that bluegills actively selected habitats to avoid competition. Because different congeners were more abundant at different depths, the form as well as the intensity of interspecific competition should have been quite different among habitats. In this case, different bluegill phenotypes should have selected the habitat where their relative fitness was greatest.

The contagious sampling distribution for bluegills (noted in

Chapter III) suggests that social interactions such as aggression were not important in determining the distribution of phenotypes among habitats. Observations of schools of bluegill fry by Werner (1969), and observations of schools of I+ and older fish by Hall and Werner (1977) also indicates that bluegills are gregarious. However, intraspecific factors may still have been important in determining the distribution of phenotypes. Rather than through aggressive encounters, the density of bluegills in each habitat may have influenced habitat utilization among phenotypes.

Fretwell and Lucas (1969) proposed a mechanism of habitat selection based on suitability of habitats and density of individuals in each habitat. They suggested that individuals should initially select the most suitable habitat. However, as density increases in the preferred habitat the suitability decreases, until eventually, a less preferred (at the beginning) habitat is equally suitable and would then be utilized. Analysis of minnow trap catches did not reveal any successive filling of habitats, instead, each year when the first adequate sample size (> 11) was collected, yoy bluegills were already widely distributed among habitats. Nonetheless, bluegill densities within habitats may have caused the observed associations between phenotype and habitat. The faster growth rates of fish in shallow, vegetated habitats suggests that this habitat might be the most suitable for all phenotypes. However, if we assume that all phenotypes are not equal competitors in shallow water, then we would expect that the inferior phenotypes would move to less suitable habitats, where they would actually increase their relative fitness because of fewer conspecifics.

The fact that growth rates were not equal among fish from all

habitats implies that not only does fitness vary between phenotypes within a habitat, but fitness (in terms of growth rate) varies between habitats. Darwinian fitness (in terms of the number of eventual offspring) was not addressed in the present study. Since meristic characters were generally not significantly different among habitats, and because phenotypes were largely defined by body form (which is not readily comparable between age groups differing greatly in size) no conclusions can be reached regarding long term survival (overwinter) of different phenotypes.

Since selection pressures were apparently different among habitats, the observed morphological variation of bluegills could have contributed to the broad niche of this species. Van Valen (1965) hypothesized that phenotypic variation results from adaptations to various habitats within a patchy environment. However, Rothstein (1973) suggested that such variation is not the result of adaptation but rather it is a result of a relaxation in stabilizing selection. If stabilizing selection were relaxed in Lake Rush, morphological variation would be great but there should not be any apparent association between specific phenotypes and habitats. Because there were specific associations between habitats and phenotypes, I conclude that variation in body form of bluegills contributes directly to a broader niche for this species.

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VITA[2]

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